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Changes in catch rates and length and age at maturity, but not growth, of an estuarine plotosid (*Cnidoglanis macrocephalus*) after heavy fishing

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Abstract—The hypothesis that heavy fishing pressure has led to changes in the biological characteristics of the estuary cobbler (*Cnidoglanis macrocephalus*) was tested in a large seasonally open estuary in southwestern Australia, where this species completes its life cycle and is the most valuable commercial fish species. Comparisons were made between seasonal data collected for this plotosid (eeltail catfish) in Wilson Inlet during 2005–08 and those recorded with the same fishery-independent sampling regime during 1987–89. These comparisons show that the proportions of larger and older individuals and the catch rates in the more recent period were far lower, i.e., they constituted reductions of 40% for fish ≥430 mm total length, 62% for fish ≥4 years of age, and 80% for catch rate. In addition, total mortality and fishing-induced mortality estimates increased by factors of ~2 and 2.5, respectively. The indications that the abundance and proportion of older *C. macrocephalus* declined between the two periods are consistent with the perception of long-term commercial fishermen and their shift toward using a smaller maximum gill net mesh to target this species. The sustained heavy fishing pressure on *C. macrocephalus* between 1987–89 and 2005–08 was accompanied by a marked reduction in length and age at maturity of this species. The shift in probabilistic maturation reaction norms toward smaller fish in 2005–08 and the lack of a conspicuous change in growth between the two periods indicate that the maturity changes were related to fishery-induced evolution rather than to compensatory responses to reduced fish densities.

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The intense harvesting of a fish stock can be accompanied by changes in certain life history traits of that stock. For example, after heavy exploitation, Atlantic cod (*Gadus morhua*) in the northwestern Atlantic and haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf matured at smaller sizes and younger ages (Olsen et al., 2004, 2005; Neuheimer and Taggart, 2010). Because earlier maturing individuals are more likely to reproduce before capture than late maturing individuals, such changes could have been the result of selection for the genotype for maturation at a smaller size or younger age (Marshall and Browman, 2007). It is relevant, however, that the results of simulation studies indicated that, although the harvesting of both immature and mature individuals and also only immature individuals of a stock leads to selection for a reduction in length and age at maturity, the restriction of harvesting to only mature individuals produces the reverse effect (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004).

Laboratory studies have shown that extreme selective harvesting of the largest individuals of Atlantic silverside (*Menidia menidia*) over four generations led to a reduction in growth rate (Conover and Munch, 2002) and that this trend was reversed over five generations when harvesting was relaxed (Conover et al., 2009). The above reduction in growth was attributed to the selection of individuals with genotypes for slower growth, whereas the subsequent increase in growth was related to the removal of those strong selection pressures. Although the above experiments are important in that they reveal that selection can lead to changes in growth, such researchers as Hilborn and Minte-Vera (2008) and Brown et al. (2008) considered that they introduced more extreme selection pressures in their experiments than are likely to be encountered by wild populations and did not take into account the type of density-dependent effects that might be experienced by such populations. On the basis of a meta-analysis of 73 commercially fished stocks of marine species, Hilborn and Minte-Vera (2008) concluded that there was no conspicuous overall trend for growth to either increase or decrease in relation to fishing intensity. Furthermore, their simulation studies indicated that the selectivity patterns of most commercial fisheries would be unlikely to result in substantial evolutionary changes in growth.

The results of several studies indicate that the growth of certain species can alter in response to changes in their density. For example, the growth of porbeagle (*Lamna nasus*) increased following a marked decline in the abundance of this species due to heavy exploitation (Cassoff et al., 2007) and, on the basis of data for eight populations, the growth of immature walleye (*Sander vitreus*) was estimated to have increased 1.3 times when abundance was low rather than high (Venturelli et al., 2010). Furthermore, the growth of Atlantic herring (*Clupea harengus*) on the Georges Bank in the northwestern Atlantic decreased when the abundance of that stock rose after the collapse of that fishery (Melvin and Stephenson, 2007). Although these authors concluded that such changes in growth were related to changes in density, such density-dependent phenotypic expressions are likely to occur only when there is strong competition for a limited supply of food or other essential resources (Brander, 2007).

Maturation reaction norms, which describe the probability that a fish will mature as a function of its length and age, have been used to assess whether changes in the length and age at maturation of some species are likely to be due to genotypic or phenotypic influences, or both (Stearns and Koella, 1986; Heino et al., 2002a, 2002b; Dieckmann and Heino, 2007). For example, this approach has shown that the maturation reaction norm for European plaice (*Pleuronectes platessa*) shifted toward younger ages and smaller lengths with intensive exploitation, indicating that short-term phenotypic responses were overlaid by a longer-term genetic response (Grift et al., 2003).

In none of the previous studies had the question of whether the biological characteristics of a stock of a species have changed in response to fishing pressure been investigated by using fishery-independent data for a heavily fished species whose life cycle is confined to an estuary. The estuary cobbler (*Cnidoglanis macrocephalus*), which is endemic to southern Australia and represented by discrete populations in estuaries (Laurenson et al., 1993a; Ayvazian et al., 1994), is the greatest contributor to the overall value of the commercial estuarine fishery on the south coast of Western Australia (Smith and Brown[1]) and is a major component of the ichthyofaunal communities of seasonally open estuaries in this region (Chuwen et al., 2009a). The vast majority of the catch of this benthic plotosid is taken in Wilson Inlet, and long-term, experienced commercial fishermen have become increasingly concerned that the abundance of large *C. macrocephalus* has declined during recent years (McIntosh[2]; Miller[3]).

The collection of sound biological data for *C. macrocephalus* in Wilson Inlet in 1987–89 (Laurenson et al., 1993a, 1993b, 1994) provided an excellent opportunity to replicate that fishery-independent sampling regime in 2005–08, and thus elucidate whether the biological characteristics of this plotosid have changed in a manner that would be consistent with continued heavy exploitation. Because individuals of the population of *C. macrocephalus* complete their entire life cycle within Wilson Inlet, we had the particular advantage of sampling the full distribution of that population. Initial comparisons between the fishery-independent data for 1987–89 and 2005–08 confirmed the opinion of commercial fishermen that the prevalence of larger (and thus probably older) *C. macrocephalus* and the abundance (catch rate) of this species declined between the two periods. These comparisons also revealed that the decline in abundance of *C. macrocephalus* in Wilson Inlet was matched by, and consistent with, a corresponding increase in fishing mortality. In view of these findings, focus was subsequently placed on elucidating 1) whether the increased and heavy exploitation of *C. macrocephalus* in Wilson Inlet was accompanied by a reduction in the length and age at maturity; and 2) whether growth changed between the two periods. Reaction norms relating the probability of maturation to length and age were examined to elucidate whether these norms changed in a way that would be consistent with genetic rather than phenotypic changes.

Materials and methods

Sampling regime

Cnidoglanis macrocephalus was sampled in each season between winter 2005 and autumn 2008 at the same six sites in the Wilson Inlet basin that were sampled between winter 1987 and autumn 1989 (Laurenson et al., 1993a, 1993b, 1994). These sites included two that were in the small region closed to commercial fishing and four that were open to such fishing (Fig. 1). The data derived from these samples were used to compare the catch rates and mortality during the two periods. Additional samples were collected from other sites (Fig. 1) to augment the numbers used for determining the length and age at maturity and growth. Note that, to ensure comparability between periods, the raw fishery-independent data obtained during 1987–89 were used to estimate the catch rates, mortality, length and age at maturity, and growth of *C. macrocephalus* in that period in precisely the same manner as that employed for the corresponding data collected during 2005–08.

At each site during 2005–08, nearshore, shallow waters of Wilson Inlet were sampled with a seine net, and

[1] Smith, K., and J. Brown. 2008. South coast estuarine managed fishery status report. *In* State of the fisheries report 2007/08 (W. J. Fletcher and K. Santoro, eds.), p. 216–223. Dept. Fisheries, Perth, Western Australia.

[2] McIntosh, O. 2009. Personal commun. Commercial fisherman, P.O. Box 565, Denmark, Western Australia, 6333.

[3] Miller, W. 2009. Personal commun. Commercial fisherman, Crusoe Beach Road, Denmark, Western Australia, 6333.

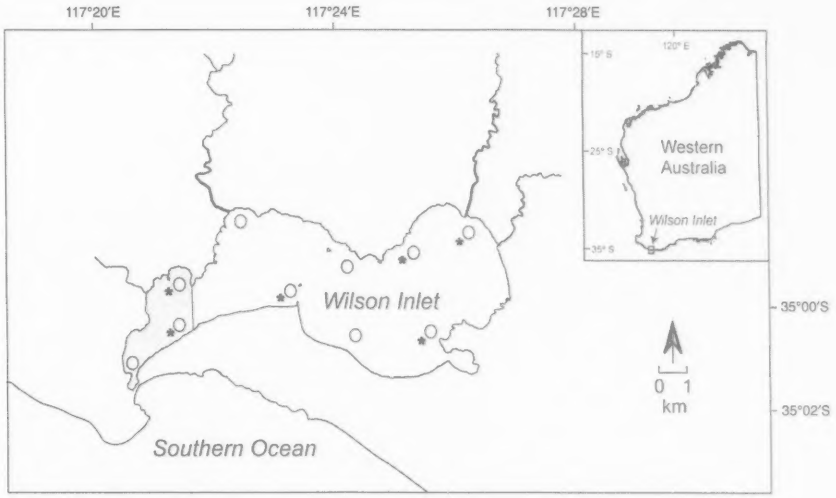

Figure 1

Map showing the location of Wilson Inlet on the south coast of Western Australia and the ten sites sampled for estuary cobbler (*Cnidoglanis macrocephalus*) during 2005–08 (O) and the six also sampled in 1987–89 (*). Hatching represents the area closed to commercial fishing.

offshore, deeper waters were sampled with gill nets and traps baited with the river prawn *Macrobrachium idae*. The seine net, which was 21.5-m long and consisted of two 10-m long wings (6 m of 9-mm mesh and 4 m of 3-mm mesh) and a 1.5-m bunt of 3-mm mesh, was laid parallel to the shore and then hauled on to the beach. This net fished to a depth of 1.5 m and swept an area of ~116 m^2. The sunken composite multifilament gill net comprised six 20-m panels, each with a height of 2 m, but containing a different stretched mesh size, i.e., 35, 51, 63, 76, 89, or 102 mm. The traps were 500×250×250 mm and contained two funnel entrances 50 mm in diameter. Gill nets and traps were set at dusk and retrieved ~12 hours later around dawn. Fishes were euthanized in an ice slurry immediately after capture. Seasonal values for salinity, water temperature, and dissolved oxygen concentration in Wilson Inlet are given in Chuwen et al. (2009b).

Catch rates

The catch rate for *C. macrocephalus* at each site on each sampling occasion during 1987–89 and 2005–08 was expressed as the number of fish caught overnight (~12 h) in a gill net comprising six panels that were of the same length (20 m) but different mesh sizes (see above). Because spawning peaks in December, thus leading to the recruitment of the new year class in January, comparisons between the catch rates in the earlier and later periods were restricted to using the samples collected seasonally between the summer and spring of 1988, 2006, and 2007, years in which data were obtained at the same sites in open and closed fishing waters in each season (Fig. 1). Analysis of variance (ANOVA) was used to determine whether the catch rates with gill nets in Wilson Inlet were significantly related to year, season, and region (open vs closed waters), each of which were considered fixed factors. Before analysis, catch rates were fourth-root transformed, which was shown to be appropriate from the relationship between the $\log_{10}$ of the standard deviation and the $\log_{10}$ of the mean catch rates of the replicate samples obtained seasonally from each region in each year.[4] The catch rates, derived from data collected in the winter and spring of 1987 and the summer and autumn of 1989, were then compared with those for the corresponding seasons during 2005–08 to ascertain whether the results obtained for these more restricted periods paralleled those based on seasonal data for full years. Mean catch rates and 95% confidence limits (CL) were back-transformed before being plotted or reported.

Age determination

The total length (TL) of each *C. macrocephalus* was measured to the nearest 1 mm and its two lapillus otoliths were removed, cleaned, dried, and stored. One otolith from each fish was placed in a black dish, covered with methyl salicylate, and its clearly defined translucent zones were counted under reflected light with a dissecting microscope. Previous work by Laurenson et al. (1994) had validated that a single translucent zone is laid down annually in the lapillus otoliths of *C. macrocephalus*. The age of each fish was estimated by the number of trans-

[4] Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed., 172 p. PRIMER-E, Plymouth, UK.

lucent zones in its otolith, the date when newly formed translucent zones typically become delineated from the otolith periphery, i.e., December–January (Laurenson et al., 1994), the date of capture of the fish, and the birth date, represented by the peak date of spawning, i.e., 1 December (Laurenson et al., 1993a).

Gillnet selectivity and mortality

Gillnet mesh selectivity values for *C. macrocephalus*, which were required to eliminate possible selection bias in research samples of age composition, were calculated for the composite gill net by using the method and model described by Kirkwood and Walker (1986). The function describing selectivity for fish of different lengths by gillnet panels with different mesh sizes is determined by fitting gamma distributions to the length compositions of fish caught in each of the range of different mesh sizes in the gill net. The means of the gamma distributions are assumed to have a linear relationship with mesh size.

The probability distribution function of a variable x that has a gamma distribution is

$$\left\{ x^{\alpha} \exp(-x/\beta)/\Gamma(\alpha+1) \right\}/\beta^{\alpha+1},$$

where α and β are the parameters of this distribution. The mode of the distribution is at $x=\alpha\beta$, and the variance is $(\alpha+1)\beta^2$. Kirkwood and Walker (1986) define θ_1 as the constant of proportionality between the modal length and mesh size m, i.e., $\alpha\beta=\theta_1 m$, and assume that the variance of the distribution is constant over the different mesh sizes, denoting this by θ_2. By relating this variance to the equation for the variance of the gamma distribution, Kirkwood and Walker (1986) advise that

$$\beta = -0.5\left\{ \theta_1 m - \left(\theta_1^2 m^2 + 4\theta_2\right)^{0.5} \right\}.$$

The fishing-induced mortality (F) of fully vulnerable fish was estimated by using the age composition data derived from gillnet sampling in 1988 and 1989 and in 2006, 2007, and 2008. The model used for this analysis, which is described in detail below, was based on the relative abundance model described by Deriso et al. (1985). Because mature males of *C. macrocephalus* excavate burrows before the spawning period and protect their small juveniles within those burrows, the data used to estimate F were restricted to those collected in late summer (February) and autumn (May) to eliminate the possible effects of such behavior on the age composition of this population. For this model a constant known level of natural mortality (M) is assumed, i.e., the value for the estimate calculated from the maximum age recorded for *C. macrocephalus* by employing Hoenig's (1983) equation for natural fish mortality.

It was assumed that fish longer than the minimum legal length (MLL) for retention (i.e., 430 mm TL) are fully exposed to a constant level of fishing mortality, whereas those that were shorter than the MLL experience no fishing mortality and are affected only by natural mortality. Thus, the age composition of the population within the estuary will reflect this pattern of fishing mortality. However, the age composition of the population was assumed to be influenced not only by natural and fishing mortality, but also by interannual variability in recruitment strength. Thus, the number of fish of age a and year class y in year t may be assumed to be represented by

$$N_{a,y,t} = \begin{cases} R_y & \text{if } a = a_1 \\ R_y \exp\left[-\sum_{j=a_1}^{a-1} Z_j \right] & \text{if } a > a_1 \end{cases}, \quad (1)$$

where R_y = the annual recruitment (to age a_1) for year class y (where $y=t-a$);
a_1 = the first age present in the age-composition data; and
$Z_a=M+F_a$ = the total mortality experienced by fish of age a.

The fishing mortality of fish of this age is zero if the length of fish at the midpoint of the ages in the age class is less than the MLL, otherwise $F_a=F$, the fishing mortality of fully vulnerable fish. The above equation for $a>a_1$ may be rewritten as

$$N_{a,y,t} = R_y \exp\left[-M(a-a_1)\right] \exp\left[-F \sum_{j=a_1}^{a-1} S_j \right], \quad (2)$$

where S_a = the selectivity of the fishing gear used in commercial fishing and it is assumed that $S_a=0$ if the length of fish at the midpoint of the ages in the age class is less than the MLL, otherwise $S_a=1$.

Denoting the expected count of fish of age a caught from year class y in year t by $\hat{c}_{a,y,t}$, we may express this as

$$\hat{c}_{a,y,t} = I_t S_a^* N_{a,y,t},$$

where I_t is a factor that represents a combination of the catchability of the fully vulnerable fish and the fishing effort used to collect the research sample in year t, i.e., the sampling intensity in that year, and S_a^* is the selectivity of the research fishing gear used for collecting the age composition data.

Thus,

$$\log_e \hat{c}_{a,y,t} = \log_e I_t + \log_e S_a^* + \log_e R_y - M(a-a_1) - F \sum_{j=a_1}^{a-1} S_j,$$

where the summation term is set to zero if $a=a_1$.

The cumulative sum of the age-dependent selectivities of the commercial fishing gear to which the stock was exposed before age a, i.e., from age a_1 to age a–1, may be written as

$$K_a = \sum_{j=a_1}^{a-1} S_j$$

for $a > a_1$ and $K_{a_1} = 0$, and we may express this model as

$$\log_e \hat{c}_{a,y,t} = \log_e I_t + \log_e S_a^* + \log_e R_y - M(a - a_1) - FK_a.$$

If we assume that M, S_a^*, and S_a are known, then the observed counts of fish within the various age classes for each sampling year may be considered to be random variates drawn from Poisson distributions, the means of which may be calculated with the above equation. Thus, with R software (R Development Core Team, 2008), Poisson regression analysis was used to fit the above model to the age-composition data for *C. macrocephalus* collected in each period and thereby to obtain estimates (and standard errors) of both the relative year class strengths and the fishing mortality reflected in those data. Because the sampling intensity employed in the different years was constant, it was removed from the model. Profiles of the residual deviances versus fishing mortality were constructed for each period by fitting the model to a set of fixed values of F over a wide range and by recording the resulting estimate of residual deviance for each value of F. Approximate 95% CLs for F were then selected as those values less than and greater than the maximum likelihood estimate of F and which produced residual deviances different from that at the maximum likelihood estimate by a value equal to $\chi^2_{0.05}(1)$ i.e., 3.84.

Length and age at maturity

The gonads of each fish were identified macroscopically as either ovaries or testes, or as indeterminate in the case of juvenile fish with very small gonads. On the basis of their macroscopic characteristics and the scheme of Laevastu (1965), the gonads of each fish were allocated to one of the following eight stages of gonadal development: I–II=immature or resting adult; III=developing; IV=maturing; V=prespawning; VI=spawning; VII=spent; and VIII=recovering spent.

Because gonads at stages I and II could not be distinguished morphologically, we could not use the macroscopic appearance of gonads to differentiate between virgin fish and fish that may have already spawned. However, the trends exhibited by the prevalences of the different gonad stages of fish caught in sequential months before and during the spawning period indicated that the gonads of the larger fish, e.g., greater than the length at which 95% of fish are mature (L_{95}), would almost invariably have been destined to progress through to stage VIII if the fish had survived. This point is substantiated by the fact that the maturity ogives, derived by using gonads at stage III or higher during the spawning period as the indicator that a fish will become or has reached maturity during that period, have asymptotes of 100% (see *Results* section). In other words, during the spawning period, the gonads of any fish remaining in the stage I–II category are virgin gonads, i.e., stage I. Fish that possessed gonads at stages III–VIII during the spawning period were classified as mature.

In each season, the gonads of up to 20 females, covering a wide range of lengths and the full suite of gonadal stages observed in that season, were retained and prepared for histological examination. For this purpose, a portion of the mid-region of one ovarian lobe was placed in Bouin's fixative for ~48 hours and dehydrated in a series of increasing concentrations of ethanol. The ovarian portions were then embedded in paraffin wax, cut transversely into 6 mm sections and stained with Mallory's trichrome. The stages in oocyte development in each ovarian section were then determined by examination with a Leica MZ7.5 dissecting microscope (Leica Microsystems, Wetzlar, Germany) to validate that each ovary had been assigned to the appropriate stage on the basis of its macroscopic appearance.

The lengths (L_{50} and L_{95}) and ages (A_{50} and A_{95}) at maturity were estimated for the females of *C. macrocephalus* in Wilson Inlet during 2005–08 and, with the raw data of Laurenson et al. (1993a), also for 1987–89. In the case of fish lengths, logistic regression analysis was used to fit curves to the probabilities that female fish at each length during that year's spawning period would possess gonads at one of stages III–VIII and were thus mature or destined to become mature during that spawning period. The logistic equation describing the probability of an individual possessing mature gonads, P, at length, L, was

$$P = \left[1 + \exp\left(-\log_e(19)(L - L_{50})/(L_{95} - L_{50})\right)\right]^{-1},$$

where the parameters L_{50} and L_{95} are the total lengths at which 50 and 95% of the individuals, respectively, would be expected to possess gonads at stages III–VIII.

On the basis of its length, the likelihood of the jth fish possessing or not possessing gonads at stages III–VIII was calculated as P_j or $1 - P_j$, respectively. Setting $X_j = 0$ if the jth fish did not possess gonads at such a stage and setting $X_j = 1$ if it did possess such gonads, the overall log-likelihood, λ, was calculated as

$$\sum_j \left\{X_j \log_e P_j + (1 - X_j)\log_e[(1 - P_j)]\right\}.$$

The logistic equation was fitted by maximizing this log-likelihood with SOLVER in Excel (Microsoft Corp., Redmond, WA). The data were randomly resampled and analyzed to create 1000 sets of bootstrap estimates of the parameters of the logistic equation and the probabilities of females and males being mature for each of a range of specified lengths. The 95% CLs of the probability of maturity at each specified length were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The medians of the bootstrap estimates were used as the point estimates of each parameter and of the probability of maturity at each specified length. The A_{50} for the females of *C. macrocephalus* at maturity were estimated

by the same procedure outlined above, but by substituting ages for lengths.

The logistic regressions describing the lengths and ages at maturity for female *C. macrocephalus* during 2005–08 and 1987–89 were compared by using a likelihood-ratio test (Cerrato, 1990). The log-likelihood, λ, which, ignoring constants, was calculated with SOLVER in Excel as

$$\lambda = -\frac{n}{2}\log_e \frac{ss}{n},$$

where n = sample size; and
ss = the sum of squared residuals between the observed and expected lengths and ages at maturity.

The value of a test statistic, G, was then calculated as twice the difference between the log-likelihoods obtained by fitting a common curve for both periods and that obtained by fitting a separate curve for each period. The hypothesis that the lengths and ages at maturity in the two periods could be described by a single curve was rejected at the α=0.05 level of significance if $G > \chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches.

Growth

Von Bertalanffy growth curves were fitted to the lengths at age of *C. macrocephalus* at the date of capture for both 1987–89 and 2005–08. The von Bertalanffy growth equation for describing growth is $L_t = L_\infty(1-e^{(-k(t-0))})$, where L_t is the length (mm TL) at age t (years), L_∞ is the asymptotic length (mm TL) predicted by the equation, k is the growth coefficient (per year) and t_0 is the hypothetical age (years) at which fish have zero length. The parameters for the von Bertalanffy growth equation and their 95% CLs were estimated from the lengths at age of fish at the date of capture by employing the nonlinear regression routine in SPSS (IBM Corp., Somers, NY).

The von Bertalanffy growth equations for females and males were compared using the likelihood-ratio test described above. The same likelihood-ratio test was used to compare the growth of *C. macrocephalus* during the current study (2005–08) with that derived for 1987–89 from the raw data collected by Laurenson et al. (1994). Because the likelihood-ratio test identifies very small differences in growth as statistically significant for large sample sizes, emphasis was placed on the level of difference in growth that was likely to be of biological significance. Such differences were considered to exist when any of the predicted lengths at integer ages ≥1 year in the range of the dominant ages within the data, i.e., 1 to 4 years, differed by >5% of the mean of the two asymptotic lengths (see *Results* section).

Maturation reaction norms

Probabilistic reaction norms for length and age at maturation (Heino et al., 2002a; Barot et al., 2004) were determined for each period. For this purpose, logistic regression analysis was employed to relate the probability that a fish was mature to its length and age, i.e.,

$$P = \left\{1+\exp\left[-(\alpha+\beta L+\gamma A)\right]\right\}^{-1}.$$

The logistic regression equations for the two periods were compared by using the likelihood-ratio test. The probability of a fish maturing at age A was then calculated as

$$m(A,L) = \left[P(A,L) - P(A-1, L-\Delta L)\right] / \left[1 - P(A-1, L-\Delta L)\right],$$

assuming that, if a fish was of length L at age A, then, from the von Bertalanffy curve fitted to the data for the period,

$$L - \Delta L = L\exp(k) - L_\infty\left[\exp(k)-1\right].$$

Note that, in this equation, L is not assumed to be the expected length at age, but represents the length of an individual fish. By setting $m(A, L)$ and solving the equation, the value of L may be estimated for any specified value of A to determine those lengths and ages at which the probability of fish maturing was 50% and conditional on the fish being alive at those ages. The contours represented by these midpoints of the reaction norms for the two periods were plotted and overlaid by the von Bertalanffy growth curves for those periods.

Water temperatures

Because water temperatures can influence maturation or growth (or both) and thus maturation reaction norms (Neuheimer and Taggart, 2007, 2010), the possibility that temperature was greater during either 1987–89 or 2006–08 was explored. Although there were no daily recordings of water temperature for Wilson Inlet during the two periods, such data are available for air temperature at Albany in the vicinity of Wilson Inlet (Australian Bureau of Meteorology: http://www.bom.gov.au/climate/data/, accessed November 2010). One-sample t-tests with SPSS software were used to examine whether, for both the minimum and maximum temperatures, the mean of the pairwise differences between the average monthly air temperatures in corresponding months over each of the 120 consecutive months of 1980–1989 and 1998–2007 was significantly different from zero. These periods encompassed all or the vast majority of the thermal history of fish caught during the two sampling periods.

Results

Length and age compositions and catch rates

Although *C. macrocephalus* caught with research gill nets at the same sites in Wilson Inlet during 1987–89 and 2005–08 covered a similar length range, i.e., ~160

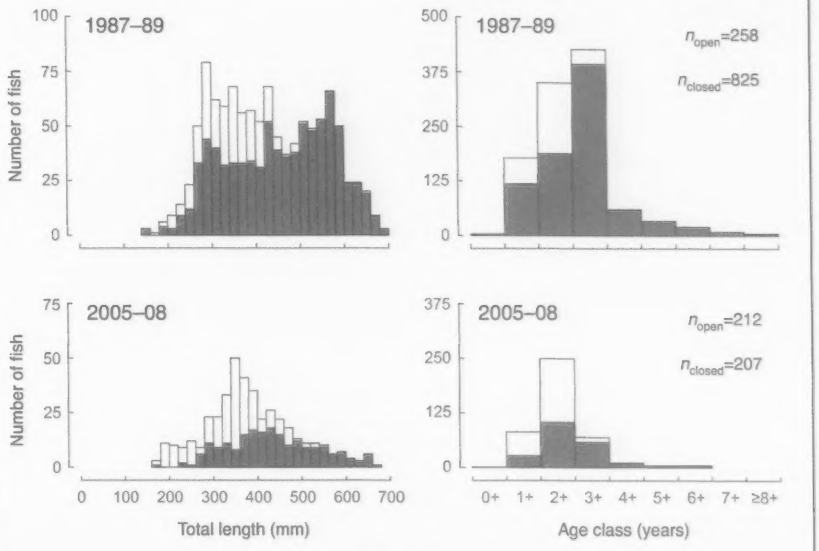

Figure 2

Length- and age-class frequency distributions for estuary cobbler (*Cnidoglanis macrocephalus*) caught with gill nets at the same sites in Wilson Inlet during 1987–89 and 2005–08. Shaded areas represent the number of individuals in each length and age class that were caught in areas closed to commercial fishing. Four sites were sampled in the area open to fishing and two sites were sampled in the closed area during both time periods (1987–89 and 2005–2008). Sample sizes (n) for the number of individuals caught in open versus closed areas are given.

to 700 mm TL, the length-frequency distribution in the earlier period contained a second strong modal length class at 560–579 mm TL, which exceeded the length of the vast majority of fish caught in the later period (Fig. 2). Consequently, the percentage of fish >430 mm TL, the current MLL for retention of this species, was far lower in 2005–08 (29%) than in 1987–89 (48%) (Fig. 2). Although the percentage of fish greater than this MLL in the waters open to commercial fishing were similarly low in both periods (12% in 1987–89 and 10% in 2005–08), the percentage of such fish was less in the area closed to commercial fishing in 2005–08 (48%) than in 1987–89 (60%) (Fig. 2).

Although the 3+ age class of *C. macrocephalus* was the best represented age class in the catches taken with gill nets during 1987–89, closely followed by the 2+ age class, the catches during 2005–08 were dominated by the 2+ age class and contained few age 3+ fish (Fig. 2). The 4+ age class was also reasonably well represented in the earlier but not the later period and the percentage of fish ≥4+ years was 11.7% during 1987–89 compared with 4.5% during 2005–08 (Fig. 2). In both periods, the vast majority of *C. macrocephalus* ≥4+ years were caught in the region closed to commercial fishing (Fig. 2).

Analyses of the catch rates of *C. macrocephalus* in each region of Wilson Inlet, i.e., sites open and closed to commercial fishing, in each season of 1988, 2006, and 2007, revealed that catch rates were significantly related to region ($P<0.001$), year ($P<0.01$), and season ($P<0.05$), and that none of the interactions between those main effects was significant (all $P>0.05$) (Table 1). The mean catch rate in the area closed to commercial fishing was 11.3 fish/12 h and far greater than in the area open to commercial fishing (1.2 fish/12 h) (Fig. 3A). Although the mean catch rate of *C. macrocephalus* in 2006 (1.9 fish/12 h) did not differ significantly ($P>0.05$) from that in 2007 (2.5 fish/12 h), both catch rates differed significantly (both $P<0.01$) from that in 1988, i.e., 12.4 fish/12 h (Fig. 3B). The mean catch rates of *C. macrocephalus* in Wilson Inlet declined from their maxima in summer and autumn (8.6 and 6.8 fish/12 h, respectively) to their minima in winter (1.3 fish/12 h) and rose again in spring (3.4 fish/12 h) (Fig. 3C). On the basis of the ANOVAs, and recognizing that there was no interaction with either region or season, we determined that the mean catch rates in the winter and spring of 1987 were greater and differed significantly from those in the corresponding seasons of 2005–08 (each $P<0.001$). Mean catch rates were also greater, but not significantly different ($P>0.05$), in four of the six comparisons between the summer and autumn of 1989 and the corresponding seasons of 2005–08.

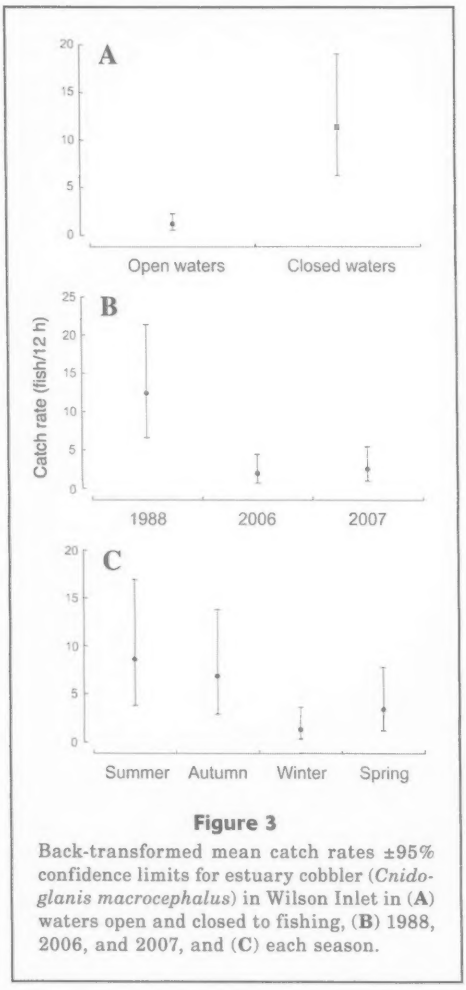

Figure 3

Back-transformed mean catch rates ±95% confidence limits for estuary cobbler (*Cnidoglanis macrocephalus*) in Wilson Inlet in (**A**) waters open and closed to fishing, (**B**) 1988, 2006, and 2007, and (**C**) each season.

Gillnet selectivity and mortality

Analyses of the mesh selectivity of the composite gill net for *C. macrocephalus* indicated that stretched meshes of 35, 51, 63, 76, 89, and 102 mm predominantly caught fish with lengths of 160–379, 190–479, 200–549, 270–619, 410–679, and 490–709 mm, respectively (Fig. 4A). The values for θ_1 and θ_2, derived from the model of Kirkwood and Walker (1986), were 6.1 and 6802, respectively. Trends in estimates of selectivity at age indicated that this species became fully susceptible to capture by the above suite of mesh sizes at ~2 years of age and essentially remained so in the immediately ensuing years (Fig. 4B).

Fishing mortality (F) in Wilson Inlet during 1988–89 was 0.57 per year (95% CL=0.27–0.90 per year) and thus far less than the 1.47 per year (95% CL=1.14–1.84 per year) estimated for the population in this estuary during 2006–08, and there was no overlap of the 95% CLs. Natural mortality (M) of *C. macrocephalus* was calculated to be 0.35 per year on the basis of a maximum age of 14 years (L. J. B. Laurenson, unpubl. data) and thus total mortality (Z) was estimated to be 0.92 per year during 1988–89 and 1.82 per year during 2006–08.

Length and age at maturity

The percent contributions of mature female *C. macrocephalus* to all females in the 400–449 and the 450–499 mm TL length classes during 2005–08 were 62% and 94%, respectively, and thus far greater than the corresponding values of 22% and 67% for 1987–89 (Fig. 5). These differences help account for the L_{50} and L_{95} of females at maturity during 2005–08, i.e., 419 mm TL (95% CL=399–438 mm TL) and 490 mm TL (95% CL=448–538 mm TL), respectively, being significantly different ($P<0.05$) from those during 1987–89, i.e., 449 mm TL (95% CL=434–463 mm TL) and 542 mm TL

Table 1

Mean squares and significance levels for three-way analysis of variance of catch rates of estuary cobbler (*Cnidoglanis macrocephalus*) derived from samples obtained with gill nets in regions open and closed to fishing in Wilson Inlet, Western Australia, in each season of 1988, 2006, and 2007. * $P<0.05$. ** $P<0.01$. *** $P<0.001$.

	Main effects			
	Region (R)	Year (Y)	Season (S)	Residual
Degrees of freedom	1	2	3	47
Mean square	9.986***	3.048**	1.312*	0.384
	Interactions			
	R×Y	*R×S*	*Y×S*	*R×Y×S*
Degrees of freedom	2	3	6	6
Mean square	0.720	0.696	0.344	0.831

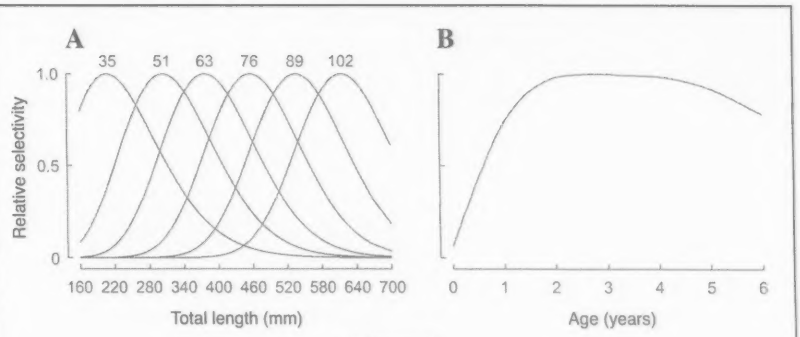

Figure 4

Relative selectivities for estuary cobbler (*Cnidoglanis macrocephalus*) (**A**) by total length for each of the various gillnet panels and (**B**) by age for the composite gill net in Wilson Inlet. Stretched mesh sizes (mm) are given above the curves in A for each gillnet panel.

(95% CL=514–569 mm TL), respectively. The percentage of females that were mature at the end of their third year of life was far greater in 2005–08 (62%) than during 1987–89 (15%) and the same was true for females at the end of their fourth year of life (95% vs 73%) (Fig. 5). Consequently, the estimates of the A_{50} and A_{95} for female *C. macrocephalus* at maturity during 2005–08, i.e., 2.9 years (95% CL=2.6–3.1 years) and 3.9 years (95% CL=3.7–4.4 years), were significantly different ($P<0.001$) from those during 1987–89, i.e., 3.5 years (95% CL=3.4–3.7 years) and 4.7 years (95% CL=4.6–5.2 years).

The number of large males caught during the spawning period was very low because, at this time, they tend to occupy burrows within which they brood eggs and rear yolk-sac larvae under their pelvic fins (Laurenson et al., 1993a). It was thus not possible to derive reliable estimates for the L_{50} or A_{50} for the males of *C. macrocephalus*.

Growth

Although the likelihood-ratio test showed that the von Bertalanffy growth curves for females and males of *C. macrocephalus* in Wilson Inlet were significantly different at the $\alpha=0.05$ level of significance (each $P<0.001$) for both 1987–89 and 2005–08, the differences in the estimated lengths at each integer age between 1 and 4 years, ages that encompassed the majority of the data, were less than 3% of the mean of the asymptotic lengths of the two growth curves for each period. The differences were thus considered not to be of biological significance. The length-at-age data for the two sexes in each period were therefore pooled. The von Bertalanffy growth curve provided a good fit to the lengths at age for all but the older *C. macrocephalus* for both 1987–89 and 2005–08; the lengths at age of the relatively small number of older fish were overestimated by the curve (Fig. 6, Table 2).

The likelihood-ratio test showed that the von Bertalanffy growth curve for *C. macrocephalus* in Wilson Inlet during 2005–08 differed significantly ($P<0.001$) from the corresponding curve derived for this species for 1987–89 (Fig. 6). However, because the differences in the estimated lengths at each integer age between ages 1 and 4 years (ages that encompassed the majority of fish) were less than 2% of the mean of the two asymptotic lengths, those differences were not considered biologically significant.

Maturation reaction norms

Logistic regression analyses demonstrated that, for both 1987–89 and 2005–08, maturity was better described as a function of length (log-likelihood [LL] = –61.2 and –21.0, respectively) than of age (LL=–102.2 and –31.2, respectively). Furthermore, the quality of the fit was not improved significantly by including age as well as length in the model (both $P>0.05$, LL=–61.2 and –20.0, respectively). Although the coefficient of the length term in the logistic curves relating the probability that a fish was mature to its length and age, i.e., β, differed significantly between the two periods ($P<0.05$), the values for the other parameters (α and γ) did not differ greatly (both $P>0.05$).

As expected, given the lack of significance of age when fitting the logistic regression equation to the combination of both length and age data, each of the reaction norms was essentially independent of age (Fig. 6). In other words, in each period, fish became mature at approximately the same length in that period regardless of their age.

The reaction norm for maturation shifted markedly toward lower lengths at age between 1987–89 and 2005–08, but the slopes of the curves did not change (Fig. 6). The von Bertalanffy growth curves did not differ in biological terms between the two periods, but because the intersection of the growth curves occurred

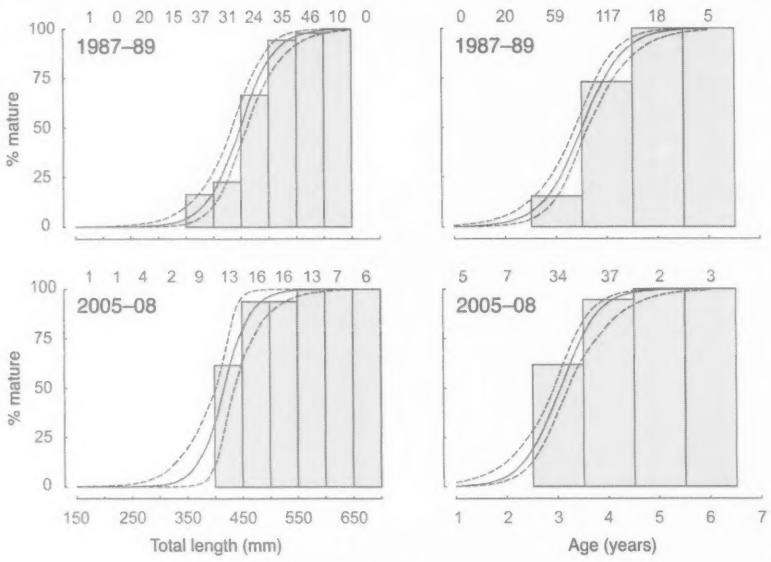

Figure 5

Percent frequencies of occurrence of mature females (ovaries at one of stages III to VIII) in sequential 50-mm total length classes and sequential age classes of estuary cobbler (*Cnidoglanis macrocephalus*) during the spawning period of this species. Logistic curves (solid lines) and their 95% confidence limits (dotted lines) were derived from logistic regression analyses of the relationship between total length and the probability that an individual fish was mature. Sample sizes for each length and age class are shown above each length and age class.

Table 2

Von Bertalanffy growth parameters and their 95% confidence limits (CL) derived from lengths at age of estuary cobbler (*Cnidoglanis macrocephalus*) caught in Wilson Inlet, Western Australia, during 1987–89 and 2005–08. L_∞=asymptotic length (mm); k=growth coefficient (per year); t_0=hypothetical age at which fish would have zero length (yr); r^2=coefficient of determination; n=sample sizes; L_{max}=maximum lengths (mm); W_{max}=maximum weights (g); and A_{max}=maximum ages (yr).

		Von Bertalanffy parameters							
		n	L_{max}	W_{max}	A_{max}	L_∞	k	t_0	r^2
1987–89		1301	722	2188	13	831	0.24	−0.09	0.86
	Lower CL					797	0.22	−0.16	
	Upper CL					864	0.26	−0.02	
2005–08		758	712	2576	8	911	0.21	−0.22	0.90
	Lower CL					839	0.18	−0.30	
	Upper CL					982	0.24	−0.14	

at different lengths and ages, the maturation at a smaller size in the later period was accompanied by a reduction in the age at maturity (Fig. 6).

Water temperatures

The mean of the pairwise differences between the average monthly air temperatures in corresponding months over each of the 120 consecutive months of the two periods did not differ significantly from zero (both $P>0.05$) for either the minimum or maximum temperature. In other words, the air temperatures were not consistently greater in one period than the other. Because Wilson Inlet is shallow, the trends exhibited by these air temperatures will be reflected closely by the water temperatures of this estuary.

Discussion

The fishery in Wilson Inlet is a multisector, i.e., commercial and, to a lesser degree, recreational, multigear, and multispecies fishery, of which the benthic *C. macrocephalus* is just one of several species targeted during commercial fishing. The data recorded by commercial fishermen for the managers of this fishery are greatly influenced by the variable extent to which the different species are targeted overall and during different periods and do not identify the fishing effort directed toward any single species. Such fishery-dependent data thus provide little information on the status of the *C. macrocephalus* stock in Wilson Inlet and how it might be changing over time. At present, such information can only be obtained from the type of fishery-independent data that were collected during the present study. The confinement of the stock of *C. macrocephalus* in Wilson Inlet to that estuary, and the availability of sound biological data for this stock in the 1980s, have provided a particularly good opportunity to explore the effects of heavy fishing on the biological characteristics of an exploited fish population. In particular, the existence of these earlier biological data allowed us to investigate the possibility that length or age at maturity, or both, changed as a result of fishing-induced evolution.

The fact that the mean catch rates of *C. macrocephalus* in Wilson Inlet during 2006–07 were 80–85% less than those in 1988 indicates that the abundance of this plotosid in this estuary declined markedly between those two periods. It is thus highly relevant that the samples during 1987–89 were dominated by age 3+ and to a lesser extent age 2+ fish and contained appreciable numbers of fish ≥4 years old and some ≥7 years old, whereas those in 2005–08 were dominated by the 2+ age class and contained very few fish older than 3 years. The smaller proportion of older fish during 2005–08 is reflected in the smaller percentage of fish caught with lengths greater than the current MLL of 430 mm TL during this more recent period, i.e., 29% vs 48%. The conclusion, based on fishery-independent data, that the numbers of large fish have declined during the last two decades, is consistent with experienced, long-term commercial fishermen responding to a reduction in their catches of larger fish by using a smaller mesh in their gill nets (McIntosh[2]; Miller[3]). Because the decline in catch rates between 1987–89 and 2005–08 was related to the marked reduction in the proportion of *C. macrocephalus* with lengths greater than the MLL for retention of this species, there is very strong circumstantial support for the conclusion that this decline was related to the effects of fishing rather than to a change in the environment.

The decline in the relative abundance of larger and older fish in Wilson Inlet between the two periods accounts for the estimates of total mortality, Z, increasing markedly from 0.92 per year during 1987–88 to 1.82 per year in 2006–08. Furthermore, fishing mortality, F, increased from 0.57 to 1.47 per year between those two periods, which represented an increase of more than 250%. Although F in the earlier period was already about 1.6 times that of natural mortality, M, it had become more than four times greater than that of M by 2006–08. The current level of F for this species in Wilson Inlet is therefore well in excess of 0.75 or 0.8 M, which have been considered target reference points for F in data-poor fisheries (Gabriel and Mace, 1999), and is thus at a level unlikely to sustain the fishery. The view that commercial fishing has led

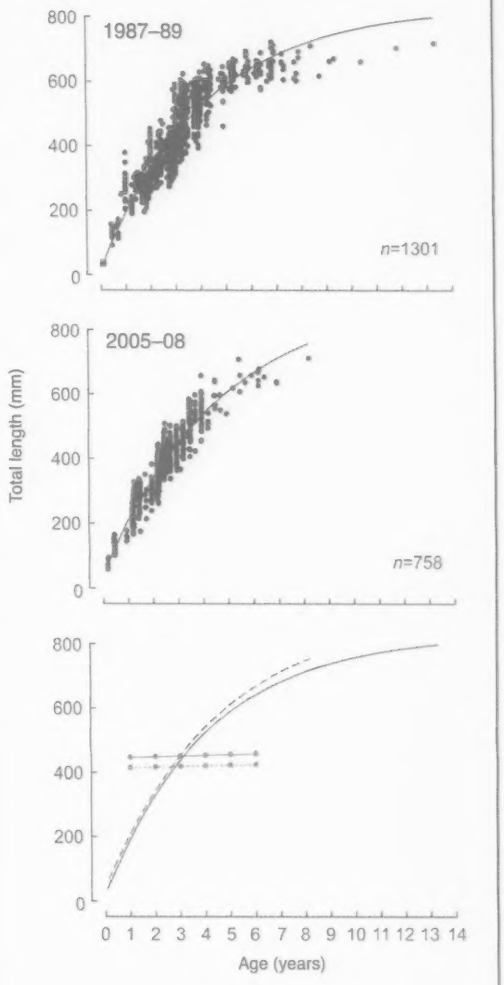

Figure 6

Von Bertalanffy growth curves fitted to lengths at age of estuary cobbler (*Cnidoglanis macrocephalus*) caught in Wilson Inlet during 1987–89 and 2005–08 and a comparison of the curves for 1987–89 (solid line) and 2005–08 (dashed line), which are overlaid with probabilistic maturation reaction norm midpoints (gray) for females at integer ages of 1–6 years. n=sample sizes.

to heavy exploitation of *C. macrocephalus* during the last two decades is supported by the observation that, although fishery-independent catch rates have fallen, the commercial catches of this species in Wilson Inlet have shown no clear tendency to decline between these two periods.[1] This finding emphasizes the difficulties in obtaining reliable values for the catch per unit of effort of a species by using fishery-dependent data for the multispecies fishery of which that species is just one contributor.

A comparison of the age-frequency data for open and closed areas indicated that the relatively small area that is closed to commercial fishing in Wilson Inlet provides some protection for the stock of *C. macrocephalus* in that estuary. Thus, although the catches in open waters contained appreciable numbers of age 1+ and 2+ *C. macrocephalus*, they yielded few age 3+ fish, whereas those in closed waters contained large numbers of 3+ individuals, the age at which this species attains, on average, the MLL of 430 mm TL for retention in the fishery. Furthermore, the catch rates, and thus relative abundances, were greater in closed than open waters.

The MLL for *C. macrocephalus* during 1987–89 was 318 mm TL, and thus considerably less than the L_{50} of 449 mm TL for females at maturity in that period. Therefore, at that time, both mature and immature individuals would have been heavily harvested, leading to selection pressures for a reduction in the length at maturity (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004). Although the MLL was increased to 430 mm TL in 1994, it is reasonable to suggest that substantial numbers of both immature and mature individuals continued to be fished, which would account for selection having led to a reduction in the L_{50} of females at maturity to 419 mm TL during 2005–08.

Comparisons between the reproductive data for *C. macrocephalus* in Wilson Inlet during the two sampling periods indicated that the females of this species matured at a smaller size and younger age during 2005–08 than during 1987–89, with respective L_{50}s of 419 and 449 mm TL and A_{50}s of 2.9 and 3.5 years. The corresponding downward shift of the reaction norms for maturation and the attainment of sexual maturity at smaller sizes and younger ages by the heavily fished *C. macrocephalus* parallel the trends exhibited by the reproductive parameters for populations of several fish species that were also heavily exploited by commercial fishing (e.g., Trippel, 1995; Olsen et al., 2004; Morita and Fukuwaka, 2007; Neuheimer and Taggart, 2010). They also parallel the patterns exhibited by natural populations of guppies (*Poecilia reticulate*) that were subjected to either high or low predation, which thus served as surrogates for the presence or absence of commercial fishing (Reznick and Ghalambor, 2005). A reduction in the size and age at maturity of heavily fished stocks may reflect an increased selection for rapidly maturing individuals because these would be more likely to reproduce before being captured (Marshall and Browman, 2007). Indeed, Olsen et al. (2005) provided evidence that the trend for earlier maturation in stocks of the heavily exploited Atlantic cod (*Gadus morhua*) halted and even showed signs of reversing after the fisheries for those stocks had been closed. The shift of the maturation reaction norms toward lower lengths indicates that there has been a genetic response of the stock of *C. macrocephalus* to the intensive exploitation to which it has been shown to have been subjected.

Although the total mortality of *C. macrocephalus* in Wilson Inlet essentially doubled between 1988–89 and 2006–08, the differences between the predicted lengths at age of fish at each of the dominant integer ages in the two periods were <2% and thus considered not to be of biological significance. This absence of a shift in growth after heavy fishing pressure is consistent with the conclusions from a meta-analysis of 73 commercially fished marine stocks that there was no evidence in general, that growth rate was related to fishing intensity (Hilborn and Minte-Vera, 2008). The lack of a clear change in growth after heavy exploitation contrasts with the situation recorded for a number of species in which growth was found to change with heavy exploitation (e.g., Cassoff et al., 2007; Melvin and Stephenson, 2007; Swain et al., 2007). Such changes have generally been attributed either to fishery-induced evolution or density-dependent effects.

Evolutionary effects would account for the reduction in growth that has been recorded for a number of heavily exploited fish populations through size-selective harvest of individuals with the genotype for fast growth (e.g., Jørgensen et al., 2007; Swain et al., 2007; Brown et al., 2008). The density-dependent alternative cause would account for the increased growth that occurs in some fish populations following heavy exploitation and which is considered to represent a compensatory response to the decline in density brought about by the removal of a large number of individuals and thus a reduction in competition for resources (e.g., Trippel, 1995; Cassoff et al., 2007). Because the marked decline in fish density of *C. macrocephalus* in Wilson Inlet between 1987–89 and 2005–08 was not accompanied by an increase in growth, this species did not undergo a density-dependent phenotypic response between the two periods. This finding, in conjunction with the change in the maturation reaction norms, supports our conclusion that the changes in the length and age at maturity of *C. macrocephalus* over time probably represent a genotypic response to fishing pressure.

Conclusions

This study provides further strong indications that heavy fishing pressure can lead to changes in the biological characteristics of fish stocks, such as maturation, and thus these biological characteristics should be considered as variables rather than constants, as has often been assumed to be the case by managers.

It is therefore important that, when such data are not already available, managers should initiate sampling regimes and analyses aimed at determining whether the biological variables for a stock are changing and, if so, take the changes into account to ensure that stock assessments and management strategies for the future are robust.

Acknowledgments

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Literature cited

Ayvazian, S. G., M. S. Johnson, and D. J. McGlashan.
1994. High levels of genetic subdivision of marine and estuarine populations of the estuarine catfish *Cnidoglanis macrocephalus* (Plotosidae) in southwestern Australia. Mar. Biol. (Heidelberg, Ger.) 118:25–31.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann.
2004. Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evol. Ecol. Res. 6:659–678.

Brander, K. M.
2007. The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. ICES J. Mar. Sci. 64:211–217.

Brown, C. J., A. J. Hobday, P. E. Ziegler, and D. C. Welsford.
2008. Darwinian fisheries science needs to consider realistic fishing pressures over evolutionary time scales. Mar. Ecol. Prog. Ser. 369:257–266.

Cassoff, R. M., S. E. Campana, and S. Myklevoll.
2007. Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. Can. J. Fish. Aquat. Sci. 64:19–29.

Cerrato, R. M.
1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47:1416–1426.

Chuwen, B. M., S. D. Hoeksema, and I. C. Potter.
2009a. Factors influencing the characteristics of the fish faunas in offshore, deeper waters of permanently-open, seasonally-open and normally-closed estuaries. Estuar. Coast. Shelf Sci. 81:279–295.
2009b. The divergent environmental characteristics of permanently-open, seasonally-open and normally-closed estuaries of south-western Australia. Estuar. Coast. Shelf Sci. 85:12–21.

Conover, D. O., and S. B. Munch.
2002. Sustaining fisheries over evolutionary time scales. Science 297:94–96.

Conover, D. O., S. B. Munch, and S. A. Arnott.
2009. Reversal of evolutionary downsizing caused by selective harvest of fish. Proc. R. Soc. Lond. B. Biol. Sci. 276:2015–2020.

Deriso, R. B., T. J. Quinn II, and P. R. Neal.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Dieckmann, U., and M. Heino.
2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. 335:253–269.

Ernande, B., U. Dieckmann, and M. Heino.
2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proc. R. Soc. Lond. B. Biol. Sci.271:415–423.

Gabriel, W. L., and P. M. Mace.
1999. A review of biological reference points in the context of the precautionary approach. *In* Proceedings of the fifth national NMFS stock assessment workshop (V. R. Restrepo, ed.), p. 34–45. NOAA Tech. Memo. NMFS-F/SPO-40.

Grift, R., A. Rijnsdorp, S. Barot, M. Heino, and U. Dieckmann.
2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. 257:247–257.

Heino, M.
1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. 55:1971–1982.

Heino, M., U. Dieckmann, and O. R. Godø.
2002a. Measuring probabilistic reaction norms for age and size at maturation. Evolution 56:669–678.
2002b. Estimation of reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES J. Mar. Sci. 59:562–575.

Hilborn, R., and C. V. Minte-Vera.
2008. Fisheries-induced changes in growth rates in marine fisheries: are they significant? Bull. Mar. Sci. 83:95–105.

Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–903.

Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus., D. S. Boukal, K. Brander, B. Ernande, A. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino, and A. D. Rijnsdorp.
2007. Managing evolving stocks. Science 318:1247–1248.

Kirkwood, G. P., and T. I. Walker.
1986. Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australian waters. Aust. J. Mar. Freshw. Res. 37:689–697.

Laevastu, T.
1965. Manual of methods in fisheries biology, 50 p. FAO, Rome.

Laurenson, L. J. B., F. J. Neira, and I. C. Potter.
1993a. Reproductive biology and larval morphology of the marine plotosid *Cnidoglanis macrocephalus* (Teleostei) in a seasonally closed Australian estuary. Hydrobiologia 268:179–192.

Laurenson, L., I. Potter, R. Lenanton, and N. Hall.
1993b. The significance of length at sexual maturity, mesh size and closed fishing waters to the commercial fishery for the catfish *Cnidoglanis macro-*

cephalus in Australian estuaries. J. Appl. Ichthyol. 9:210–221.

Laurenson, L. J. B., I. C. Potter, and N. G. Hall.
1994. Comparisons between generalized growth curves for two estuarine populations of the eel tailed catfish *Cnidoglanis macrocephalus*. Fish. Bull. 92:880–889.

Law, R., and D. R. Grey.
1989. Evolution of yields from populations with age-specific cropping. Evol. Ecol. 3:343–359.

Marshall, C. T., and H. I. Browman.
2007. Introduction: Disentangling the causes of maturation trends in exploited fish populations. Mar. Ecol. Prog. Ser. 335:249–251.

Melvin, G. D., and R. L. Stephenson.
2007. The dynamics of a recovering fish stock: Georges Bank herring. ICES J. Mar. Sci. 64:69–82.

Morita, K., and M. Fukuwaka.
2007. Why age and size at maturity have changed in Pacific salmon. Mar. Ecol. Prog. Ser. 335:289–294.

Neuheimer, A. B., and C. T. Taggart.
2007. The growing degree-day and fish size-at-age: the overlooked metric. Can. J. Fish. Aquat. Sci. 64:375–385.
2010. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? Can. J. Fish. Aquat. Sci. 67:854–865.

Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann.
2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935.

Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey, and U. Dieckmann.
2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 62:811–823.

R Development Core Team.
2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reznick, D. N., and C. K. Ghalambor.
2005. Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 62:791–801.

Stearns, S. C., and J. C. Koella.
1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893–913.

Swain, D. P., A. F. Sinclair, and J. M. Hanson.
2007. Evolutionary response to size-selective mortality in an exploited fish population. Proc. R. Soc. Lond. B. Biol. Sci. 274:1015–1022.

Trippel, E. A.
1995. Age at maturity as a stress indicator in fisheries. BioScience 45:759–771.

Venturelli, P. A., N. P. Lester, T. R. Marshall, and B. J. Shuter
2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. Can. J. Fish. Aquat. Sci. 67:1057–1067.

Regional and seasonal patterns of epipelagic fish assemblages from the central California Current

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Abstract—The coastal Pacific Ocean off northern and central California encompasses the strongest seasonal upwelling zone in the California Current ecosystem. Headlands and bays here generate complex circulation features and confer unusual oceanographic complexity. We sampled the coastal epipelagic fish community of this region with a surface trawl in the summer and fall of 2000–05 to assess patterns of spatial and temporal community structure. Fifty-three species of fish were captured in 218 hauls at 34 fixed stations, with clupeiform species dominating. To examine spatial patterns, samples were grouped by location relative to a prominent headland at Point Reyes and the resulting two regions, north coast and Gulf of the Farallones, were plotted by using nonmetric multidimensional scaling. Seasonal and interannual patterns were also examined, and representative species were identified for each distinct community. Seven oceanographic variables measured concurrently with trawling were plotted by principal components analysis and tested for correlation with biotic patterns. We found significant differences in community structure by region, year, and season, but no interaction among main effects. Significant differences in oceanographic conditions mirrored the biotic patterns, and a match between biotic and hydrographic structure was detected. Dissimilarity between assemblages was mostly the result of differences in abundance and frequency of occurrence of about twelve common species. Community patterns were best described by a subset of hydrographic variables, including water depth, distance from shore, and any one of several correlated variables associated with upwelling intensity. Rather than discrete communities with clear borders and distinct member species, we found gradients in community structure and identified stations with similar fish communities by region and by proximity to features such as the San Francisco Bay.

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Twenty five percent of marine fisheries catch comes from regions that encompass a mere five percent of the world's oceans: within the Benguela, California, Canary, Peru, and Somalia currents (Jennings et al., 2001). Management of these highly productive coastal upwelling ecosystems has historically been based on single species assessments, although the science informing management has long recognized the limited power of this approach. After the dramatic and unexpected collapse of several major small-pelagic fisheries worldwide circa 1945–72, scientists began to advocate the need to incorporate climate, ocean conditions, and other sources of uncertainty into management (Fréon et al., 2005; MacCall, 2009). In the last two decades the momentum to achieve this goal has increased, and some form of ecosystem-based management is now a stated policy objective of government agencies in several nations (Link et al., 2002; Ecosystem Principles Advisory Panel[1]). Ecosystem management plans have now been proposed for most U.S. fisheries including the U.S. west coast and large portions of the California Current ecosystem, and various agencies and institutions are actively collecting the biological and environmental data that will be needed to bring these plans to action (Ecosystem Plan Development Team[2]).

The high productivity of the California Current (CC) is primarily the result of local wind-driven seasonal upwelling and the interaction of alongshore currents with prominent coastal features such as capes, headlands, and bays that advect upwelled water masses into complex patterns of offshore filaments and coastal retentive eddies (Davis, 1985; Gan and Allen, 2002). The zone of maximum spring and summer wind stress and wind-driven upwelling occurs between Cape Blanco in southern Oregon (43°N) and Point Conception in central California (34°N) (Nelson, 1977). Headlands in this region including Cape Mendocino, Point Arena, Point Reyes, and Point Año Nuevo are the main locales of newly upwelled water. Bays located downcurrent act as retention zones where eddies form and trap aging upwelled water (Paduan and Rosenfeld, 1996), allowing concentrated phytoplankton blooms to develop nearshore (Vander

[1] Ecosystem Principles Advisory Panel. 1999. Ecosystem-based fishery management. A report to Congress by the National Marine Fisheries Service, 54 p. National Marine Fisheries Service, Office of Science & Technology, 1315 East-West Highway, Silver Spring, MD 20910.

[2] Ecosystem Plan Development Team. 2010. Ecosystem fishery management planning for U.S. west coast fisheries. A report to the Pacific Fisheries Management Council, 35 p. Pacific Fisheries Management Council, 7700 N.E. Ambassador Pl., Ste. 101, Portland, OR 97220.

Woude et al., 2006). Blooms in this region often occur at cape-and-bay spatial scales and are ephemeral, typically lasting several days after an upwelling wind event (Largier et al., 2006).

Coastal topographical features also affect the distribution of zooplankton and larval invertebrates in this region (Ebert and Russell, 1988; Largier, 2004). Localized differences in zooplankton density and community structure have been measured across distances of 10 km or less in the vicinity of headlands and their upwelling shadows (Graham et al., 1992; Wing et al., 1998; Mace and Morgan, 2006), and across-shelf variation in zooplankton (Morgan et al., 2003) and ichthyoplankton (Auth, 2008) community structure is well described. A complex field of mesoscale eddies and fronts off coastal Oregon in the summer of 2000 correlated spatially with four or five different zooplankton assemblages, and dynamic water-mass attributes influenced by recent strong upwelling and advection appear to be the principal factors driving horizontal planktonic distribution (Keister et al., 2009). Seasonal zooplankton shifts have been linked to intensity of upwelling and variation in the timing and delivery rate of subarctic and subtropical water onto the shelf (Peterson and Miller, 1977; Roesler and Chelton, 1987), and interannual patterns appear related to El Niño–Southern Oscillation (ENSO) events and other multiyear climate cycles that impact the ocean on basin-scales (Rebstock, 2003). The physical processes that promote rapid growth and patchiness among plankton have additional downcurrent trophic effects among krill, fishes, seabirds, and marine mammals (Ainley, 1990; Croll et al., 2005; Ware and Thomson, 2005; Jahncke et al., 2008).

Assemblage patterns of epipelagic fishes in the CC are known mostly from studies in the northern portion. Orsi et al. (2007) summarized broad-scale species associations from surface trawls in both the California and the Alaska Current, in a region spanning 1100 km of coastline and identified three or four spatially distinct assemblages. In a study covering about 400 km of coastline in Washington and Oregon, Brodeur et al. (2005) sampled across-shelf transects and described seven different fish assemblages, some of which were spatially distinct. At the finest scales yet examined for epipelagic fishes in this region, Emmett et al. (2006) found significant differences in abundance among years, months, and stations for several common predator and forage species in a region influenced heavily by the Columbia River plume. These and several prior studies (summarized in Brodeur et al., 2003) highlight the scales of variation found among epipelagic nekton in the northern CC, but the area south of the Oregon–California border was sampled in only a few of these studies.

The central CC supports vast schools of clupeiform fishes that are essential prey items for fish and avian predators. Food-web models constructed for the CC ecosystem are an essential component of ecosystem-based fishery management; these models require data from surveys of forage fishes and their associates, details of the spatial and temporal structure of their populations, and measurement of the oceanographic variables that drive local abundance (Field et al., 2006; Samhouri et al., 2009). This area is also home to several large state and federal marine sanctuaries and is one of the primary testing grounds for Marine Protected Areas (MPAs) in the United States. Although these MPAs are designed primarily for the conservation of demersal fish and invertebrates, knowledge of pelagic fish habitat and community structure could also be used to inform decisions on size and placement of MPAs (Reese and Brodeur, 2006).

Our study covered a strip of coastal ocean running north–south above the inner continental shelf in a region of strong seasonal upwelling off northern and central California. The region encompasses several prominent headlands and bays, a small group of offshore islands, and the outflow of the largest river in the state through the San Francisco Bay. Detailed patterns of spatial and temporal community structure of epipelagic fishes in this portion of the CC are undescribed. The objectives of this study were 1) to test for regional, seasonal, and interannual patterns of fish abundance in catch data from six years of summer and fall surface trawl surveys; 2) to identify dominant species associated with patterns of community structure, and correlate biotic patterns to a suite of water properties that may be influencing fish distribution; and 3) to provide a detailed baseline record of species abundance and distribution for the region, against which future change may be measured, and to provide primary data for ecosystem-based management for the California Current ecosystem.

Materials and methods

The study area encompassed a 185-km strip of coastal ocean between Point Arena (38°55′N) and Point San Pedro (37°35′N) in northern and central California (Fig. 1). Ocean sampling stations were located from 1 to 39 km offshore at a depth of 18–141 m mostly over the inner portion of the continental shelf and largely within the boundaries of three national marine sanctuaries (Cordell Bank National Marine Sanctuary [NMS], Gulf of the Farallones NMS, and Monterey Bay NMS). Fish obtained for this study were collected as part of a more detailed examination of Chinook salmon (*Oncorhynchus tshawytscha*) growth and energy status during their first ocean year (MacFarlane, 2010). Because Chinook salmon are thought to remain very close to shore during this life-history stage, we chose to extend our nearshore north–south coverage as much a possible. This spatial arrangement of stations restricted our analysis to tests of primarily along-shelf latitudinal patterns, with less emphasis on onshore–offshore gradients.

We divided our study area into two geographic regions, the north coast (NC) and the Gulf of the Farallones (GF), separated by a prominent headland at Point

Reyes (38°00′N) (Fig. 1). Point Arena defined the northern border of NC, and Pt. San Pedro the southern border of GF. The boundaries of the GF are generally well recognized, and similar borders have been reported elsewhere (Ainley, 1990; MacFarlane et al., 2005). We worked from chartered commercial trawlers and the NOAA ship *David Starr Jordan*. Samples were collected over 5–13 consecutive days in June or July (hereafter "summer" cruises) and for 5–11 consecutive days in September or October (hereafter "fall" cruises) for six years, from 2000 to 2005. All sampling was conducted during daylight hours, between sunrise and sunset. There were 23 and 11 fixed trawling stations in the NC and GF, respectively, and both regions were sampled during every cruise, although not every station was visited each time (Table 1). Effort was not equally distributed among years, seasons, or regions because of operational constraints, weather, and other project objectives.

We used a Sea-Bird SBE 19 CTD (conductivity, temperature, and depth) profiler with added sensors for hydrographic sampling conducted immediately before or after trawling at each station. Five environmental variables were measured in 1-m depth bins from the surface to the bottom: water temperature, °C (TMP); salinity, ppt (SAL); water density, kg/m^3 (DEN); photosynthetically available radiation, (µE/sec)/m^2 (PAR); and chlorophyll-*a* concentration, µg/L (CHL). Values from 1 to 15 m depth were averaged for each cast, and therefore represented about the same range as the vertical spread of the trawl net. Owing to occasional instrument failures, not all of the CTD sensor data were collected on every cast (Table 1). Bottom depth in m (DEP) and distance offshore (DIS) in km were measured for every haul.

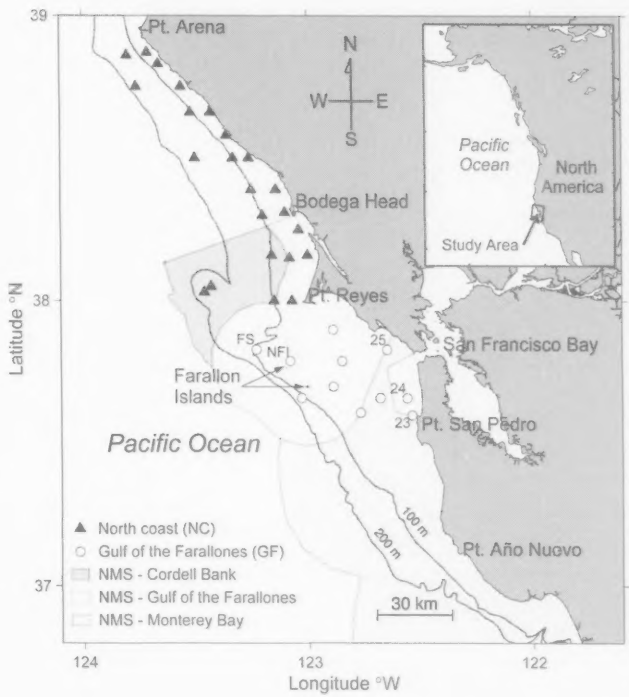

Figure 1

Location of trawl stations off central and northern California where epipelagic fish species were collected during 2000–05. Symbols show stations of the two regional sampling groups: north coast (NC) and Gulf of the Farallones (GF). Also shown are station labels for selected eastern GF (23, 24, 25) and western GF stations (FS=Fanny Shoal, NFI=North Farallon Island). Three National Marine Sanctuaries (NMS) are indicated.

Trawling and sample processing

We used a 264 Nordic rope trawl and 3.0-m^2 foam-filled pelagic doors to collect epipelagic fish and invertebrates. Net dimensions were approximately 14 m (vertical at mouth) by 27 m (horizontal at mouth) by 194 m (length). Vertical spread was measured in the field with depth recorders attached to the head and footrope, and the measurement of horizontal spread had been estimated and provided previously by the manufacturer (NET Systems, Bainbridge Island, Washington). Effective mouth area was assumed constant at 380 m^2. The codend liner was constructed of 6×10 mm knotless nylon and did not usually retain fish <40 mm total length or small invertebrates such as krill. Floats on the headrope and bridles helped maintain the net near the surface (usually within 1.0–1.5 m) continuously during tows. Sets were made at depths of ≥37 m, except at four shallower stations where the bottom was thought to be free of snags. Tow duration was 6–40 min (mean=22 min) and inversely proportional to jellyfish (*Chrysaora fuscescens* and *Aurelia* spp.) density. When abundant, these large jellyfish reduce sampling efficiency and can damage nets. Tow speed varied from 5.0 to 8.0 km/h (mean=6.5 km/h), depending on sea conditions and vessel. Tow distance was measured either with a mechanical flow meter pulled alongside the boat or calculated with GPS; tow distance varied from 0.5 to 4.8 km (mean=3.0 km).

Most fishes retained in the codend were identified to species, or occasionally to higher taxonomic levels, and counted. Larval and other small fish <40 mm were seldom retained. However, postlarval osmerids, scorpaenids, and flatfishes were occasionally captured and these were identified to family or sometimes to broader groups (e.g., "flatfish larvae"). Very large hauls were subsampled by volume or weight, and total species abundance was estimated from the composition of subsamples. Size class distinctions were made for only one species: juvenile Chinook salmon (≤250 mm fork length) were counted separately from larger individuals (>250 mm fork length, hereafter called "adults"). Adult salmon and other highly mobile species are thought to

Table 1

Number of stations sampled and hauls completed by region, year, and season, for trawl hauls and environmental variables obtained from CTD casts. Region: NC=north coast of California, GF=Gulf of the Farallones; season: S=summer, F=fall; variables: TMP=water temperature, SAL=salinity, DEN=water density, PAR=photosynthetically available radiation, CHL=chlorophyll-*a* concentration, DEP=water depth, DIS=distance of station from shore.

Region	Year	Season	Stations	Hauls	TMP	SAL	DEN	PAR	CHL	DEP	DIS
NC	2000	S	1	1	1	1	1	0	1	1	1
		F	2	2	2	2	2	2	0	2	2
	2001	S	2	2	2	2	2	2	2	2	2
		F	6	6	5	5	5	1	5	6	6
	2002	S	6	6	5	5	5	5	5	6	6
		F	10	11	10	10	10	10	10	11	11
	2003	S	11	11	11	11	11	11	11	11	11
		F	11	13	13	13	13	13	13	13	13
	2004	S	17	17	17	17	17	16	17	17	17
		F	21	21	21	21	21	20	21	21	21
	2005	S	22	24	24	24	24	24	24	24	24
		F	17	17	16	16	16	16	16	17	17
GF	2000	S	4	6	4	4	4	2	4	6	6
		F	6	8	7	7	7	5	2	8	8
	2001	S	5	7	6	6	6	6	6	7	7
		F	3	5	4	4	4	1	4	5	5
	2002	S	6	10	9	9	9	9	9	10	10
		F	5	8	6	6	6	6	6	8	8
	2003	S	5	8	6	6	6	6	6	8	8
		F	7	10	10	10	10	9	10	10	10
	2004	S	5	8	5	5	5	5	5	8	8
		F	4	6	5	5	5	5	5	6	6
	2005	S	5	6	6	6	6	6	6	6	6
		F	4	5	5	5	5	5	5	5	5

be undersampled because they avoid the net (Emmett et al., 2006), although at times they were captured in large numbers. Macroinvertebrates—primarily jellyfish, squid, ctenophores, and salps—although often abundant in the catch, were not consistently identified or counted and therefore are not included here. To account for differences in tow distance and duration, fish abundance was standardized to a volume of 10^6 m^3 for all hauls—a standard that is about equal to a typical tow of 30 minutes at 5.6 km/h (3.0 knots).

Individual hauls were often sparse in diversity, sometimes containing only one or two species. For this reason, it was necessary to combine all hauls into larger sample groupings to run statistical tests and produce meaningful ordinations. Because sampling effort was not equal among stations, regions, or years, averaging the standardized abundance of each species (rather than pooling) was the appropriate method to cumulate hauls. For regional and seasonal comparisons, hauls at each station were averaged across all six years to obtain species abundance (averaged for each station) for each season and region. For interannual comparisons, hauls were grouped more broadly, by averaging for region and season within each of the six years separately. The analytical methods we used were robust to the inclusion of rare species and unaffected by zero values in the community matrix, so that the full species matrix was used throughout the study, thus avoiding arbitrary omissions. Standardized abundances were square-root transformed to mildly reduce the disproportionately large influence of highly abundant species in the community analysis.

Assemblage structure: tests and ordinations

We used multivariate statistical tests and ordinations to search for patterns of community structure in space and time. PRIMER analytical software (vers. 6.1.6, PRIMER-E Ltd, Plymouth, U.K.) with PERMANOVA+ (Anderson et al., 2008) was used for all multivariate routines. We first tested for differences among main effects (regions, years, and seasons) and interaction terms by using a type-III permutational multivariate analysis of variance (PERMANOVA) with hauls averaged by region, year, and season in a three-way crossed design. PERMANOVA is a semiparametric group difference test directly analogous to multivariate analysis of variance but with pseudo-*F* ratios and *P*-values generated by resampling (permutation) the resemblance measures of the actual data; thus it is less sensitive to assumptions of parametric tests that are frequently violated by community data sets (Anderson, 2001; Anderson et al., 2008). For all biotic

data we used the Bray-Curtis coefficient to construct resemblance matrices. The variance components and degrees of freedom of highly nonsignificant interaction terms in the full model were consolidated by sequentially pooling them with the residuals to generate the final reduced model. Regions and seasons were treated as fixed effects: the examination and testing of variations in community structure between regions and seasons was the *a priori* objective of the study. Years were treated as random effects because there was no *a priori* reason for the timing or duration of the study: years have no particular meaning except to serve as replicates for the fixed effects of primary concern. Moreover, interannual patterns may be complicated by other sources of uncontrolled variation such as weather and sea state, or different ships and captains.

To examine community patterns in finer detail (specifically, among all four combinations of the two fixed factors [2 regions×2 seasons]), we used a two-way crossed PERMANOVA type-III design with hauls averaged by station and season across all six years. This method of cumulating samples provided greater replication and more degrees of freedom for each factor than was possible in the previous three-way arrangement. After this global test, pairwise comparisons were made between the two levels of each significant factor.

We used nonmetric multidimensional scaling (MDS), an unconstrained ordination technique, to create graphical summaries of relationships among samples based on the abundance of the various species present and to highlight spatial and temporal patterns of community structure. Unlike PERMANOVA, MDS operates on the rank orders of the elements in the resemblance matrix, rather than on the resemblance matrix itself, and constructs a map of the samples in a specified number of dimensions. The axes in MDS plots have no meaning other than for orientation, and scaling in MDS plots, if shown, is arbitrary. A stress value ranging from 0 to 1.0 is used to measure the reliability of the ordination, with zero indicating a perfect fit and all rank orders correctly represented by the relative distance between all pairs of points in the graph, and with values >0.3 indicating that points are close to being arbitrarily placed in the graph (Clarke and Warwick, 2001).

Where group differences in community structure were found (α<0.05 in PERMANOVA tests), we used another exploratory method to identify those species most responsible for the difference. For any two groups, SIMPER (similarity percentages) calculates the percent contribution each species makes to the total between-group dissimilarity (Clarke and Warwick, 2001). SIMPER identifies a small subset of species that are more consistently present or more abundant in one group than another, thus helping to reveal the major contributors to each group's biotic identity and simplifying the interpretation of community patterns. Because the routine incorporates both abundance and frequency of occurrence, it allows species at low abundance to be major contributors to community patterns if they are consistently present in one place or time.

Water properties: tests and ordinations

To match the approach used for the community analysis, we also ran multivariate tests for group differences in environmental structure using PERMANOVA and graphically summarized the relationships among hydrographic samples using ordination—in this case principal components analysis (PCA). In order to make direct comparisons with the biological patterns, oceanographic variables were grouped, averaged, and plotted in the same arrangements as those used for hauls in the species analysis. Because we were interested in examining water properties only as they relate to biotic patterns, the starting point for the PERMANOVA environmental model was the reduced model from the biotic analysis, with all three main effects included and all interaction terms pooled with residuals. Four variables with skewed distributions required transformation before PCA, and appropriate transformations were selected by using log-likelihood profiles of Box-Cox transformations. A square-root transformation was used for DIS and PAR, and a $\log_{10}(x)$ transformation for DEP and CHL. Environmental variables were normalized before PCA analysis, and Euclidian distance was used to measure sample similarity.

Oceanographic variables were also individually tested for regional and seasonal differences by using univariate analysis of variance (ANOVA) type-II tests. The same transformations described above were applied. After transformation, the distributions of all environmental variables met the requirements necessary for parametric testing and ANOVA was an appropriate choice in this instance.

The degree of similarity between corresponding species and environmental patterns was measured by using a matrix-matching permutation test (the BIO-ENV routine in PRIMER). With this procedure, biotic and abiotic samples are compared from matching locations and a subset of water properties are determined that maximize their correlation to the community pattern (Clarke and Warwick, 2001). To accomplish this goal, the elements of the two corresponding sample similarity matrices (Bray-Curtis for biotic and normalized Euclidian distance for abiotic) are ranked, the ranks are ordered by sample number or location, and the two matching sets of ordered ranks are compared by calculating a correlation coefficient—in this case the familiar Spearman coefficient (ρ_s). The significance level of the match is determined by comparing the observed value of ρ_s to a large set of ρ_s values generated by repeated random reassignment of sample labels in one of the two similarity matrices. Only samples that are jointly present in both matrices are considered in the test.

Results

We caught a total of 53 different species of fish during this study, of which a few common mid-trophic level

Table 2

Results of permutational multivariate analysis of variance (PERMANOVA) pairwise tests for differences in fish assemblages and environmental variables between regions of the north coast (NC) of California and the Gulf of the Farallones (GF) for both seasons, and between summer and fall for both regions.

			Fish assemblages		Environmental variables	
Factor	Level	Pairs	pseudo-*t*	*P*	pseudo-*t*	*P*
Season	summer	NC, GF	2.05	0.0001	1.80	0.0149
	fall	NC, GF	2.17	0.0001	3.26	0.0001
Region	NC	summer, fall	2.69	0.0001	2.30	0.0022
	GF	summer, fall	1.03	0.3471	2.04	0.0073

fishes heavily dominated the catch. One hundred and thirty-one hauls were taken in summer and fall cruises along the NC. The catch in that area was dominated numerically by jacksmelt (*Atherinopsis californiensis*, 39%) and Pacific herring (*Clupea pallasii*, 39%), with smaller landings of northern anchovy (*Engraulis mordax*, 6%), juvenile Chinook salmon (5%), and surf smelt (*Hypomesus pretiosus*, 2%). The five most frequently captured species were juvenile Chinook salmon (60%), jacksmelt (48%), adult Chinook salmon (34%), medusafish (*Icichthys lockingtoni*, 30%), and Pacific sardine (*Sardinops sagax*, 21%).

Eighty-seven hauls were taken in summer and fall cruises in the GF. Species composition was dominated numerically by northern anchovy (45%) and Pacific herring (44%), followed by jacksmelt (4%), Pacific sardine (4%), and whitebait smelt (*Allosmerus elongates*, 2%). The five most frequently captured species in this region were juvenile Chinook salmon (55%), Pacific herring (44%), jacksmelt (33%), adult Chinook salmon (32%), and medusafish (31%).

Although the interpretation of yearly patterns along the NC (but not the GF) was hampered somewhat by the increasing sample size over time in the north, the haul-averaged catch density indicated that 2004 and 2005 stand out as unusual years for several of the common species (those with >15% frequency of occurrence) (Appendix 1). In the NC, the average density of jacksmelt was much higher in both seasons in 2004 and 2005 than at any other time; Chinook salmon (both juveniles and adults) and Pacific herring average density was highest in summer of 2004 and 2005; northern anchovy and Pacific sardine density was highest in fall of 2004 and 2005; and jack mackerel (*Trachurus symmetricus*) were captured only in 2004 (both seasons) and during the summer of 2005. In the GF, the average density of jacksmelt was especially high in the fall of 2004 and during both seasons in 2005, sardine density was especially high in spring of 2004 and 2005, anchovy density was above average in both seasons in 2005, and Pacific butterfish (*Peprilus simillimus*) average density was highest in both seasons in 2005. No common species were notably absent in these two years.

Multivariate biotic patterns

All interaction terms in the three-way PERMANOVA were highly nonsignificant ($P>0.40$); these terms were sequentially removed by pooling their components of variation and degrees of freedom with residuals to increase statistical power for the remaining terms in the final reduced model. Main effects in the reduced model were all significant (region: pseudo-$F_{1,16}=6.14$, $P=0.0001$; season: pseudo-$F_{1,16}=2.07$, $P=0.0334$; year: pseudo-$F_{5,16}=1.52$, $P=0.0293$). The two-way PERMANOVA for regional and seasonal community differences was also highly significant for both main effects (region: pseudo-$F_{1,60}=7.60$, $P=0.0001$; season: pseudo-$F_{1,60}=4.62$, $P=0.0001$) and not significant for *region*×*season* interaction (pseudo-$F_{1,60}=1.30$, $P=0.196$). Subsequent pairwise comparisons (Table 2) showed strong differences in community structure between the NC and GF regions for both seasons, and strong seasonal differences within the NC region. However, there was no apparent seasonal difference within the GF region, where summer and fall communities were not statistically distinguishable.

Interannual community pattern The ordination of trawl catch averaged broadly by region, year, and season (Fig. 2A) showed clear separation of samples by region, but other differences due to years and seasons are not well supported by this configuration. With the exception of one point ('04 GF-summer), 2004 and 2005 occupied a separate quadrant of the data cloud, indicating that there may have been some commonality of structure shared by those two years alone. Samples from the remaining four years did not show an annual pattern at this level of resolution. Seasonal (summer vs. fall) samples also appeared to be randomly mixed in this configuration, especially for the GF region. Seasonal differences in community structure must be examined at a finer scale of resolution, and samples averaged more narrowly by station and season across all six years, for recognizable seasonal patterns in MDS plots to emerge.

Regional community pattern Ordinations of samples averaged by station and season visually supported the result of the two-way PERMANOVA and subsequent

pairwise comparisons. In MDS plots of community structure, stations in summer cruises separated fairly well by region (Fig. 3A), with NC stations forming a central cloud and GF stations scattered more widely around the perimeter and mostly to one side of the plot. Within the GF region there was further recognizable spatial structure: stations 23, 24, and 25 are the three easternmost nearshore stations, closest to the mouth of the San Francisco Bay in real space. Stations FS (Fanny Shoal) and NFI (North Farallon Island), the two westernmost GF stations, were dissimilar in the summer ordination. Stress was moderate at 0.13, indicating a fairly reliable plot. Samples from fall cruises formed a similar regional pattern, with NC stations falling in a (mostly) separate central cloud surrounded by more widely scattered and dissimilar GF stations (Fig. 3B). Further spatial structure within the GF was again apparent; the eastern nearshore trio of stations (23, 24, and 25) were placed together and opposite most of the remaining GF stations. The two westernmost GF stations (FS and NFI) were structurally similar to each other in fall. Stress was moderate at 0.19.

Seasonal community pattern Ordinations of seasonal community patterns also supported their corresponding statistical tests. Along the NC there was clear separation of summer and fall samples (Fig. 3C), consistent with the significant seasonal test for this region, whereas in the GF there was broad overlap of summer and fall samples (Fig. 3D) consistent with the nonsignificant test for seasonal differences in this area. Summer samples in both regions were more widely spread across the plots, and hence more variable, than fall samples, and stress was moderate for both plots.

Representative species The SIMPER routine identified a small subset of species most responsible for the observed differences between the NC and GF communities, and between summer and fall communities along the NC (Table 3). Over 80% of the total dissimilarity between communities was attributed to about 12 species, and six of these were high ranking contributors to all three of the paired SIMPER comparisons between significantly different communities. Variation in the relative abundance and frequency of occurrence of these six species, in particular, allowed the multivariate tests and ordinations to discriminate among groups. For example, the three common clupeiform species (Pacific herring, Pacific sardine, and northern anchovy) were much more abundant in the GF than along the NC, regardless of season. Among the other principal species, jacksmelt and juvenile Chinook salmon were more abundant in the NC-summer community, whereas medusafish were more abundant in the GF-summer community. In the fall, juvenile Chinook salmon were still more abundant in the NC community, and jacksmelt and medusafish were more abundant in the GF.

Significant seasonal differences were only observed along the NC. Here, the NC-summer community was dominated by jacksmelt, Pacific herring, and juvenile Chinook salmon, and the NC-fall community was dominated by northern anchovy, Pacific sardine, and medusafish. Other important contributors to regional dissimilarity were adult Chinook salmon, jack mackerel, and Pacific saury (*Cololabis saira*) (all more strongly associated with the NC), and Pacific tomcod (*Microgadus proximus*), surf smelt, and Pacific butterfish (all more strongly associated with the GF). Along the NC, adult Chinook salmon and jack mackerel were more abundant in summer than in fall, whereas Pacific tomcod were more abundant in fall than in summer.

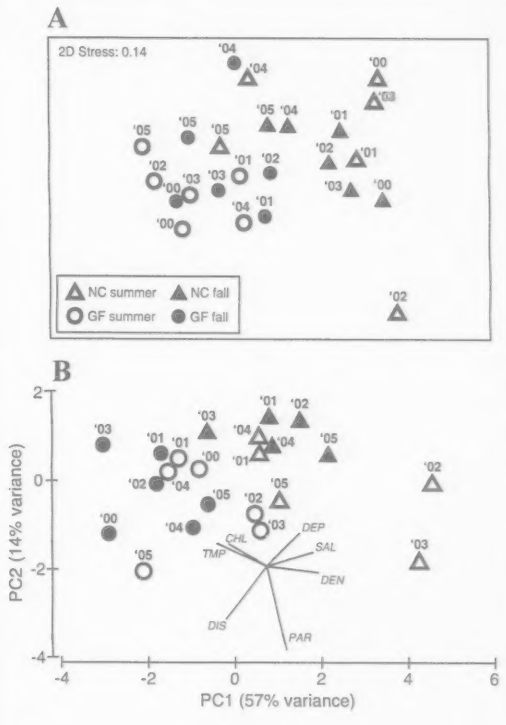

Figure 2

(**A**) Nonmetric multidimensional scaling (MDS) plot of aggregated trawl samples averaged and coded by region, season, and year. Data represent square-root transformed fish densities; resemblance was based on ranked Bray-Curtis similarity. (**B**) Principal components analysis (PCA) plot of seven aggregated environmental variables: chlorophyll-*a* concentration, water density, water depth, distance offshore, photosynthetically available radiation, salinity, and water temperature: log(CHL), DEN, log(DEP), sqrt(DIS), sqrt(PAR), SAL, and TMP, respectively, measured immediately before or after trawling, and averaged and coded by region, season, and year. Individual variable transformations were applied to improve normality; resemblance was based on Euclidian distance.

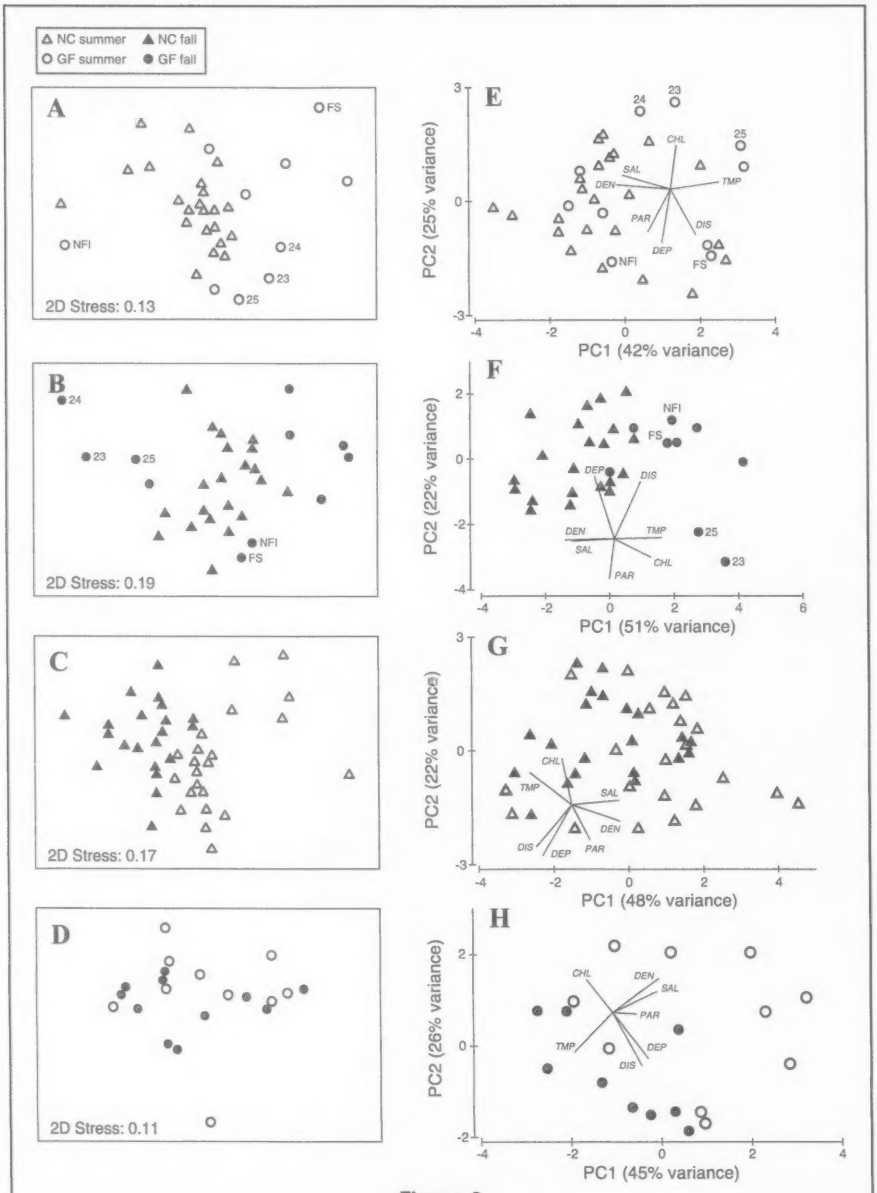

Figure 3

(**A–D**) Nonmetric multidimensional scaling (MDS) plots of aggregated trawl samples averaged by season and station across all years, and coded by region and season. Data are square-root transformed fish densities; resemblance based on ranked Bray-Curtis similarity. (**E–H**) Principal components analysis (PCA) plots of seven aggregated environmental variables: chlorophyll-*a* concentration, water density, water depth, distance offshore, photosynthetically available radiation, salinity, and water temperature: log(CHL), DEN, log(DEP), sqrt(DIS), sqrt(PAR), SAL, and TMP, respectively, measured immediately before or after trawling, averaged by season and station across all years, and coded by region and season. Individual variable transformations were applied to improve normality; resemblance was based on Euclidian distance. Selected Gulf of the Farallones stations are labeled: eastern nearshore (23, 24, 25) and western offshore (FS=Fanny Shoal, NFI=North Farallon Island) groups.

Table 3

Species contributions to between-group dissimilarity for three pairs of communities with significantly different community structures (i.e., $\alpha<0.05$ in pairwise PERMANOVA tests), determined by using the SIMPER (similarity percentages) routine. Species are listed in order of decreasing percent dissimilarity contribution with an 80% cumulative dissimilarity cutoff imposed. Abundance is the untransformed average number of fish/10^6 m^3 within each group: NC=north coast, GF=Gulf of the Farallones, S=summer, F=fall. Dominant (Dom.) region and dominant (Dom.) season indicate the region and season, respectively, where each species was more abundant in each of the three comparisons presented. For the species Chinook salmon: ad=adult (>250 mm fork length); jv=juvenile (≤250 mm fork length).

Species	Dissimilarity	Contribution	NC abundance	GF abundance	Dom. region
Summer NC vs. summer GF, Σ(dissimilarity)=86.38					
Pacific herring, *Clupea pallasii*	18.10	20.96	127.46	1644.41	GF
jacksmelt, *Atherinopsis californiensis*	15.48	17.92	99.12	55.56	NC
Pacific tomcod, *Microgadus proximus*	7.23	8.36	0.08	8.94	GF
Pacific sardine, *Sardinops sagax*	5.95	6.88	0.07	184.68	GF
Chinook salmon, jv, *Oncorhynchus tshawytscha*	5.47	6.33	13.70	9.48	NC
northern anchovy, *Engraulis mordax*	4.89	5.66	0.06	2166.27	GF
medusafish, *Icichthys lockingtoni*	3.80	4.40	0.28	1.65	GF
Chinook salmon, ad, *Oncorhynchus tshawytscha*	3.51	4.06	2.20	2.07	NC
jack mackerel, *Trachurus symmetricus*	3.27	3.79	2.91	0.00	NC
surf smelt, *Hypomesus pretiosus*	2.65	3.07	6.40	6.82	GF
Fall NC vs. fall GF, Σ(dissimilarity)=81.04					
Pacific herring, *Clupea pallasii*	16.11	19.88	0.30	756.19	GF
northern anchovy, *Engraulis mordax*	14.64	18.07	17.30	204.83	GF
jacksmelt, *Atherinopsis californiensis*	13.91	17.17	24.42	184.51	GF
Chinook salmon, jv, *Oncorhynchus tshawytscha*	5.75	7.09	2.90	1.79	NC
medusafish, *Icichthys lockingtoni*	5.08	6.27	2.74	2.80	GF
Pacific sardine, *Sardinops sagax*	4.85	5.98	3.22	6.92	GF
Pacific saury, *Cololabis saira*	3.41	4.21	4.71	0.82	NC
Pacific butterfish, *Peprilus simillimus*	3.16	3.90	0.42	2.43	GF

Species	Dissimilarity	Contribution	Summer abundance	Fall abundance	Dom. season
Summer NC vs. fall NC, Σ(dissimilarity)=75.35					
jacksmelt, *Atherinopsis californiensis*	17.24	22.88	99.12	24.42	S
Pacific herring, *Clupea pallasii*	10.89	14.46	127.46	0.30	S
northern anchovy, *Engraulis mordax*	7.16	9.51	0.06	17.30	F
Chinook salmon, jv, *Oncorhynchus tshawytscha*	6.70	8.88	13.70	2.90	S
Pacific sardine, *Sardinops sagax*	4.47	5.93	0.07	3.22	F
jack mackerel, *Trachurus symmetricus*	4.23	5.62	2.91	0.48	S
medusafish, *Icichthys lockingtoni*	3.82	5.06	0.28	2.74	F
Chinook salmon, ad, *Oncorhynchus tshawytscha*	3.54	4.70	2.20	0.39	S
Pacific tomcod, *Microgadus proximus*	2.26	3.00	0.08	0.91	F

Water properties

The analysis of environmental structure was designed to mirror the community analysis. Samples were averaged, tested, and plotted in the same arrangements in order to facilitate direct multivariate comparison of ocean conditions and community patterns. Interaction terms in the three-way PERMANOVA for differences in environmental structure were consolidated with residuals before tests were run, and all main effects in the reduced model were found to be significant (region: pseudo-$F_{1,14}$=8.08, P=0.0002; season: pseudo-$F_{1,14}$=2.58, P=0.0438; year: pseudo-$F_{5,14}$=1.88, P=0.0352). The two-way PERMANOVA for regional and seasonal differences was also highly significant for both main effects (region: pseudo-$F_{1,59}$=10.92, P=0.0001; season: pseudo-$F_{1,59}$=8.58, P=0.0001) and not significant for *region×season* interaction (pseudo-$F_{1,59}$=1.47, P=0.20). All subsequent pairwise comparisons were highly significant (Table 2).

Interannual hydrographic pattern The ordination of hydrographic variables averaged broadly by region, year, and season (Fig. 2B) showed clear separation of samples by region, but failed to show evidence of other groupings due to years or seasons at this scale of resolution. Unlike the corresponding MDS community plot, the years 2004 and 2005 did not occupy a distinct quadrant of the PCA environmental plot.

Regional hydrographic pattern Stations in summer cruises did not form clearly distinct regional groups based on PCA (Fig. 3E). Rather, GF stations overlapped broadly with those of the NC, and weak regional separation was apparent on a gradient described mostly by PC1 axis. Most GF stations fell on the right of the first axis (characterized by higher TMP, lower SAL, and lower DEN) and most NC stations fell on the left (characterized by the opposite conditions). The trio of eastern nearshore GF stations (23, 24, and 25) was again placed together and was characterized by higher CHL and lower DIS, DEP, and PAR than other summer stations. Stations in fall cruises (Fig. 3F) showed greater regional separation than summer stations. This division also fell along an environmental gradient captured mostly by the first axis, with the GF characterized by higher TMP, higher CHL, lower DEN, and lower SAL, and the NC characterized by the opposite conditions. The finding that water properties within the two regions were more dissimilar in fall than in summer was consistent with PERMANOVA pairwise tests. One GF station (number 24) and two NC stations were excluded from the fall analysis because of incomplete CTD data sets.

Seasonal hydrographic pattern Summer and fall samples along the NC overlapped broadly but on average occupied mostly different sides of their PCA plot (Fig. 3G) and separated primarily along a gradient described by PC1; most summer samples were characterized by higher SAL and DEN and lower TMP than fall samples. Summer and fall samples in the GF (Fig. 3H) showed greater separation on the PC1 gradient, composed of roughly equal parts DEN, SAL, and TMP and capturing most of the seasonal variance. Summer samples in both regions were more variable than fall samples.

Univariate pattern ANOVA tests showed that water properties varied significantly between regions for six of the seven variables and between seasons for four variables (Fig. 4). TMP increased from north to south and from summer to fall, indicating stronger coastal upwelling in summer and north of Pt. Reyes. CHL also increased significantly from north to south, but the seasonal pattern was not consistent in the two regions and summer and fall differences in CHL were not significant. SAL and DEN were positively correlated (r^2=0.97, P<0.001) and showed similar patterns, with higher values along the NC and a significant decrease from summer to fall in both regions. PAR was the only variable not significantly different between regions, but it was significantly higher in summer than in fall. DEP and DIS varied regionally but not seasonally. On average, GF stations were shallower and farther from shore, reflecting the broader shelf in the GF. The interaction between region and season was not significant for any of the variables, although it was close for TMP (P=0.06) and PAR (P=0.08).

Relationship of environment to community structure

The ordination of samples based on species similarity (Fig. 2A) was structurally related to the ordination of samples based on environmental similarity (Fig. 2B), as determined by direct comparison of their underlying similarity matrices with the BIO-ENV routine. Using first the full set of seven environmental variables with the BIO-ENV protocol, we found significant similarity of multivariate pattern between the biotic and the environmental data (ρ_s=0.439, P=0.001). However, a reduced subset of these seven variables generated an improved match with the community pattern. The solution that maximized the Spearman rank correlation between the two resemblance matrices was a four-variable combination of DEP, DIS, TMP, and SAL (ρ_s=0.471, P=0.001) that performed slightly better than the full seven-variable comparison. Closely following this four-variable solution were three three-variable combinations (DEP, DIS, DEN; DEP, DIS, TMP; DEP, DIS, SAL) that gave ρ_s-values only slightly smaller than the four-variable combination. These three are arguably the best solutions because they achieve essentially the same level of correlation with one less variable.

Discussion

Abundance data from a six-year survey of coastal marine fishes captured in surface trawls revealed significant differences in community structure based on region, year, and season. These patterns were mirrored by differences in a small suite of mostly physical oceanographic variables collected along with the biotic samples, indicating that epipelagic fish communities were responding to interannual, seasonal, and relatively small-scale spatial variability in oceanography. Multivariate ordination placed samples with similar fish communities in arrangements that corresponded with a boundary somewhere in the vicinity of the headland at Pt. Reyes. GF stations were more dispersed and variable in ordinations than NC stations, and the plotted arrangement of several GF stations appeared to be influenced by their common proximity to features such as the San Francisco Bay outflow and possibly the Farallon Islands. Differences in community structure were due primarily to differences in relative abundance and occurrence of about 6–12 ubiquitous species, most of which were regularly caught in both regions and during both seasons of the study. Thus, community patterns were not driven by abrupt turnover of dominant taxa across regional boundaries or between seasons, but rather by gradients in local abundance. Most of the dominant species identi-

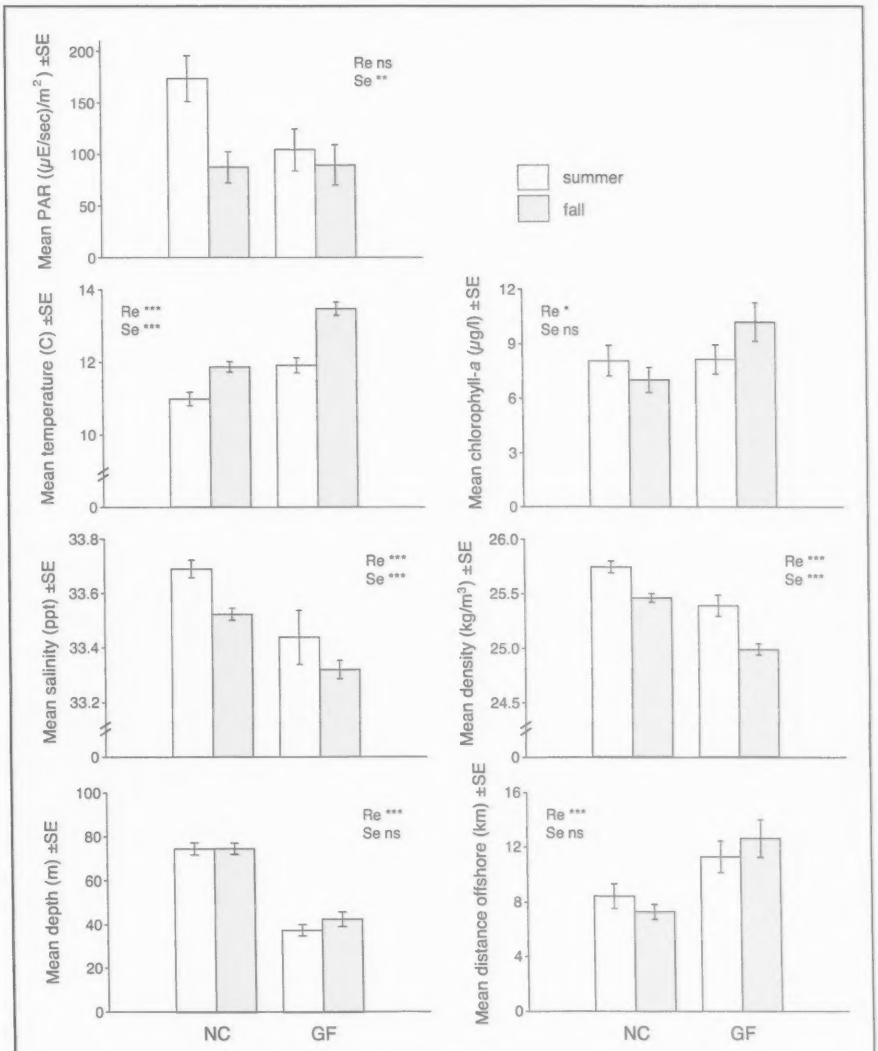

Figure 4

Environmental variables measured immediately before or after trawling at stations off northern and central California, averaged by region and season across years and shown here untransformed. NC=north coast, GF=Gulf of the Farallones. Significance levels for two-way analysis of variance (ANOVA) tests were determined separately for each variable and are represented in each graph: Re=region, Se=season, ns= not significant at $P>0.05$, *$P\leq0.05$, **$P\leq0.01$, ***$P\leq0.001$. All Re×Se interaction terms were not significant.

fied by the SIMPER routine were typical of more than one assemblage, which is not surprising for communities consisting of mobile pelagic species.

The arrangement of stations in PCA plots, based solely on environmental measures, was broadly similar to MDS ordinations based on fish abundance and diversity. Because the resemblance matrices underlying the corresponding PCA and MDS plots were independently derived, the match is unlikely to be purely coincidental. It is reasonable to assume that one or more of the oceanographic variables are potentially causal factors affecting fish community structure in this region. Matrix-matching tests, where community patterns were compared to oceanographic features, helped narrow the field down to three or four important variables, namely DEP, DIS, and any one or two of the upwelling-related variables TMP, SAL, and DEN, which together proved to be fairly good indicators of variation in the commu-

nity. Future studies of a possible link between middle and upper trophic level community structure and pelagic ocean habitats in this region could expand our efforts with the inclusion of additional hydrographic variables (e.g., dissolved oxygen, nitrates, silicates, turbidity, and frontal intensity). The relationship between zooplankton abundance and fish community structure is of particular interest. For example, cold-water copepod biomass has been shown to correlate strongly with survival of age-1 northern anchovy and may ultimately determine adult anchovy density (Litz et al., 2008).

In the most comprehensive study of nekton community structure and oceanography off Oregon and Washington to date, Brodeur et al. (2005) identified a larger set of water properties with significant correlations to fish assemblages. In their study, differences in community structure were primarily related to seven environmental variables associated with distance offshore and upwelling intensity: water depth and temperature, water transparency, chlorophyll concentration, and three different macronutrients. The authors propose that future studies could develop a single metric combining multiple oceanographic variables as a means of quantifying suitable habitats for pelagic species. Among the other surface trawl surveys in the CC during which environmental variables were measured, onshore–offshore differences in fish community structure were usually present, but north–south patterns were weak or absent. Several oceanographic features that vary with distance offshore (depth, temperature, salinity, and turbidity) were correlated with species distributions (Emmett et al., 2006). In a study describing the physical properties of biological hotspots in the coastal zone off southern Oregon, Reese and Brodeur (2006) found that distance offshore, water depth, temperature, density, and salinity accounted for the strongest correlations with species ordination axes, although the order of importance among these physical variables was different among years and seasons and chlorophyll was of little value in explaining community structure. Curiously, although the hotspots themselves persisted, the fish species inhabiting them did not. The authors found different sets of indicator species within each of two hotspots on four separate cruises. In all of these studies, an area farther offshore than that of the present study was sampled, usually at least to the shelf break.

Our catch was dominated by a few highly abundant mid-trophic level species, as is typical of temperate upwelling zones worldwide. Examples include *Engraulis mordax* and *Sardinops sagax* in the California Current, *E. ringens* and *S. sagax* in the Peru Current, *E. capensis* and *S. ocellatus* in the Benguela Current, and *E. encrasicholus* and *Sardina pilchardus* in the Canary Current (Parrish et al., 1983). Chief among these "forage" species in our study were northern anchovy and Pacific herring; lesser contributions were made by jacksmelt and Pacific sardine, depending on location and season. Northern anchovy composed more than half of the overall catch and were abundant in both regions but ranked seventh overall in frequency of occurrence, indicating large but scattered schools. Northern anchovy abundance in surface trawls was also notably high and variable off Oregon (Brodeur et al., 2005; Litz et al., 2008), and larval anchovy were the most abundant fish in plankton samples from the Columbia River plume (Parnel et al., 2008). In midwater trawls off central California (Pt. Reyes to Pt. Conception), Mais (1974) reported that 55% of hauls contained northern anchovy and greatest concentrations were in the south and <18.5 km offshore. In surface trawls in the northern CC, Brodeur et al. (2005) reported that Pacific herring, Pacific sardine, and northern anchovy together accounted for 76% of the catch, although their frequency of occurrence was relatively low. This pattern of clupeiform abundance was attributed to schooling behavior and patchy distribution. Subadult Chinook salmon were far less abundant in catches but were taken in a higher overall percentage of hauls, consistent with our findings and indicating a lower density and a more uniform distribution than for clupeids. In a broad survey of the CC between Vancouver Island and central California, 75% of 1.5 million fish taken in surface trawls were Pacific sardine and Pacific herring (Orsi et al., 2007). Pacific herring were positively associated with osmerids (true smelts) and juvenile salmonids, and together these three taxa (sometimes in combination with northern anchovy and other species) formed a distinct group typical of inshore habitats (Brodeur et al., 2004, 2005; Emmett et al., 2006; Orsi et al., 2007). In the present study, Pacific herring and juvenile Chinook salmon were co-dominant summer species in the NC region based on SIMPER analysis, but spatially herring were more dominant in the GF and juvenile Chinook salmon more dominant along the NC. Osmerids were far less abundant in our study than in those conducted farther north off Oregon and Washington and contributed little to the distinctions among communities in our area.

Unlike herring and juvenile salmonids, Pacific sardines are usually grouped with an offshore migratory assemblage that includes Pacific mackerel (*Scomber japonicus*) and jack mackerel off Oregon (Brodeur et al., 2003; Reese and Brodeur, 2006). These three species appear to migrate from the southern CC farther north and onshore in unusually warm years (Brodeur et al., 2005; 2006). In spite of our limited cross-shelf coverage, the consistent importance of the variables DEP and DIS in matrix-matching tests strongly indicates that onshore–offshore gradients structure fish communities in our region as well, and implies that a distinct offshore assemblage perhaps similar to that of the northern CC exists in our area. However, in classification analysis of selected species in our study (not shown), fishes typically associated with offshore habitats, such as Pacific sardine and jack mackerel, showed no clear relationship to each other or to distance offshore, and Pacific mackerel were too infrequently caught to allow assessment of their distribution. The spatial coverage of ongoing trawl surveys conducted by

the U.S. National Marine Fisheries Service (NMFS) along the northern California coast beginning in 2010 has been expanded well beyond the shelf break to help resolve this point.

During this study ocean conditions in the northern CC shifted from a phase of cool, generally productive coastal water with strong upwelling and La Niña-like conditions (2000–02) to a warmer, less productive phase with weaker upwelling and El Niño-like conditions (2003–05) (Goericke et al., 2005). This gradual but progressive shift culminated in a major oceanographic anomaly in 2005 when upwelling in the northern CC was delayed by ~2 months, during which time sea surface temperatures remained abnormally high (Peterson et al., 2006; Schwing et al., 2006). Ecosystem effects caused by this delay were dramatic and included unusually low chlorophyll (phytoplankton) levels in some areas, a crash in recruitment of intertidal mussels and barnacles, reduction and redistribution of copepods and other zooplankton, extremely low numbers of rockfish larvae, and the complete breeding failure of a krill-eating seabird (Peterson et al., 2006; Sydeman et al., 2006; Barth et al., 2007). In the epipelagic fish community off Oregon, anomalous abundance patterns were seen during 2004–05 for northern anchovy, Pacific sardine, Pacific herring, jack mackerel, osmerids, and juvenile salmonids, and several southern species were recorded far north of their usual range (Brodeur et al., 2006). In the present study we obtained larger than average catches of several common species during 2004–05, most notably along the NC. The patterns we observed were generally consistent with the catch anomalies seen in Oregon (except for juvenile salmon, where the above average densities we recorded were opposite the Oregon pattern). The years 2004 and 2005 grouped together weakly in community ordination but the hydrographic data we collected at that time failed to show a multivariate signal of an anomaly, probably because the 2005 climate event was much stronger in the northern CC off Oregon and Washington than in the central CC off California, and it had a much greater effect on more northern fish populations (Peterson et al., 2006; Schwing et al., 2006). Along the NC and especially in the GF, localized oceanographic processes operating on smaller (cape-and-bay or less) spatial scales may have been more important to the community than coastwide climate forcing, at least in the short run (i.e., the six-year period of our study) and may have masked any broader effects.

Water origins and transport patterns could account for much of the spatiotemporal variability we observed. During upwelling-favorable northwest spring winds, shelf water transport along the NC is characterized by a strong jet that originates in the Pt. Arena upwelling center and travels south over the outer shelf and slope (20–50 km from the coast), to be deflected offshore by Pt. Reyes. Inner shelf water (<20 km from the coast) derives from more localized upwelling centers along the NC and is transported south past Pt. Reyes but more slowly, whereupon it enters GF circulation or is entrained offshore (Kaplan and Largier, 2006). When upwelling-favorable winds relax, the southward-flowing offshore jet slows or stalls, while inner-shelf transport reverses direction completely and flows poleward up the coast. Gulf water is entrained in these poleward flows and travels north around Pt. Reyes toward the NC, remaining close to shore with little offshore dispersion until upwelling resumes (Kaplan and Largier, 2006). This scenario may also predominate in fall, when upwelling-favorable winds are generally absent. Thus, connectivity between the NC and the GF is punctuated by alternating water sources and directions of nearshore transport, although net transport is to the south in most years. In 2004–05 when upwelling was weak and delayed, longer periods of poleward transport of GF water toward the NC during spring and summer may have resulted, perhaps leading to the higher densities of clupeiform fishes, jacksmelt, and juvenile salmon we observed off the NC during that period.

In contrast to the NC, water transport and circulation in the GF (described by Steger et al., 2000) is characterized by persistent poleward flow of Pacific equatorial water along the shelf break and slope (40–80 km from the coast). Over the shelf (<40 km from the coast) circulation is more variable and net transport is to the south. The jet of cool upwelled water arriving from the NC slows and some portion is captured and retained in a coastal cyclonic eddy in the northern and eastern GF, where it is sheltered from wind forcing in the lee of Pt. Reyes. In the central GF, cross-shelf Ekman transport carries surface water offshore during upwelling-favorable periods and onshore during relaxation, and submesoscale (10–50 km diameter) vortices are common in all seasons. These circulating features transport and mix large volumes of different water types within the GF and their presence effectively masks any regular seasonal hydrographic patterns in some years. Up to four different water masses meet in the GF, and the frontal mixing zones between oceanic, bay outflow, upwelled cold and upwelled warm water have sinuous and shifting locations depending on the intensity of wind forcing, river volume, and other variables that change seasonally and annually (Schwing et al., 1991). Fundamentally different water circulation patterns north and south of Pt. Reyes set the GF apart as a hydrographically unique location along the northern California coast (Steger et al., 2000; Largier et al., 2006). It is also the only coastal region in California to receive substantial nutrient enrichment from a major fresh water source, here the eutrophic estuarine waters of the Sacramento River exiting through the San Francisco Bay (Wilkerson et al., 2002).

Fronts are common ocean features that form where distinct water masses collide or opposing currents meet. Long bands of concentrated flotsam, plankton, and neuston often form at surface convergent fronts, sometimes as visible meandering features. The intensity, persistence, and locations of nearshore fronts correlate positively with larval fish density (Bjorkstedt et al., 2002) and invertebrate recruitment (Roughgarden

et al., 1991). Forage and predatory fishes, seabirds, and marine mammals actively seek out and concentrate at fronts in order to feed (Olson et al., 1994; Sims and Quayle, 1998). Nearshore frontal probability, measured in fine-scale (5 km) bins, during the upwelling season in 2006 was much higher in the GF than elsewhere along the northern California coast (Woodson et al.[3])—further evidence of the unique oceanographic properties of the GF and a possible reason for the much higher density of clupeiform fishes that we recorded there, than along the NC. Wing et al. (1998) described the spatial pattern of Gulf mesoscale fronts in 1994 and 1995 and collected several taxa of larval crabs and rockfish whose distributions in the GF and along the north side of Pt. Reyes were strongly correlated with specific water masses, water movement and locations of fronts. The highest abundance of larval crabs was found in the northern GF retention zone and the highest abundance of rockfish larvae along fronts farther offshore. The catch variability and higher average fish densities that we observed in six years of trawling in the GF is consistent with this view of the region as a complex frontal mixing and retention zone downcurrent of a major headland and also indicates that adjacent coastal regions may be less complex hydrographically and thus more predictable biologically. With different water masses impinging on the Gulf from all four sides and shifting frontal boundaries in different years and seasons, a more variable pelagic community would be expected here than elsewhere.

Conclusions

In this study we provide the first detailed baseline data on epipelagic fish abundance in a highly dynamic yet less studied portion of the CC. As such it can be used to evaluate the effects of future perturbations, such as climate-induced oceanographic changes or variation in fishing pressure, on fish communities. The analytical techniques employed offer a powerful method to reveal community structure and relationships with environmental conditions, and their use in other systems is encouraged. The analyses reveal spatial and temporal gradients in community structure between two adjacent but oceanographically different regions. Our results indicate that waters within the GF and nearshore to the estuary exit are oceanographically complex transition zones in contrast to more uniform but separate coastal communities; hence they reveal the importance of the GF and similar zones elsewhere as connectors or corridors between coastal and estuarine communities, where more closely spaced biological and physical sampling is required to untangle the inherent complexity of such areas compared to open coastlines (Schwing et al., 1991). In order to move incrementally toward ecosystem-based management, the Pacific Fisheries Management Council may consider adopting a more regional "nested approach" to spatial management of living marine resources in the CC, in which smaller segments of the ecosystem could be defined for management purposes on cape-and-bay scales that better match the scales of variation in community and habitat structure (Ecosystem Plan Development Team[2]).

The gradual implementation of ecosystem-based management will continue to involve regular ship-based oceanographic and biological sampling. It will be necessary to measure species diversity within smaller cohesive regions, to account for multispecies patterns of distribution, to identify and describe essential fish habitat, and to model and understand food-web dynamics including predator-prey relationships, interspecific competition, and guild membership and biomass, among other things (Francis et al., 2007). Quantitative indicators for describing fish communities and for tracking ecosystem status are used in current modeling (Rice and Rochet, 2005). The best indicators are easily measured and are reliable proxies for a suite of desirable ecosystem attributes, and often include species that are not themselves the targets of any fishery and would likely have been ignored in previous single-species management plans.

Indicators of ecosystem status often consist of species with common properties such as foraging guild membership, spatial distribution, ecotype, or some combination of these (e.g., small planktivorous fish, migratory mesopelagic fish, all sharks) (Fulton et al., 2005). Among the best performing indicators for a set of north Pacific ecosystem models are biomass groups consisting of detritivores, flatfish, and zooplanktivorous fish, as well as some surprising compound metrics such as the ratio of forage fish to jellyfish biomass (Samhouri et al., 2009). The use of indicators such as these to track and evaluate ecosystem attributes is a central part of the integrated ecosystem assessment process and an important policy objective of the NMFS (Levin et al., 2009).

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[3] Woodson, C. B., M. A. McManus, J. A. Tyburczy, J. A. Barth, L. Washburn, J. E. Caselle, M. H. Carr, D. P. Malone, P. T. Raimondi, B. A. Menge, and S. R. Palumbi. 2011. Coastal fronts set recruitment and connectivity patterns across multiple taxa. Unpubl. manuscript, 13 p. [Available from C.B. Woodson, Environmental Fluid Mechanics Lab., Dept. Civil and Environmental Engineering, Standord Univ., Stanford, CA 94305-4020.

Literature cited

Ainley, D. G.
1990. Seasonal and annual patterns in the marine environment near the Farallones. *In* Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community (D. G. Ainley and R. J. Boekelheide, eds.), p. 23–50. Stanford Univ. Press, Stanford, CA.

Anderson, M. J.
2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M. J., R. N. Gorley, and K. R. Clarke.
2008. PERMANOVA+ for PRIMER: guide to software and statistical methods, 214 p. PRIMER-E, Plymouth, U.K.

Auth, T. D.
2008. Distribution and community structure of ichthyoplankton from the northern and central California Current in May 2004–06. Fish. Oceanogr. 17:316–331.

Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, J. M. Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce, L. Washburn.
2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proc. Natl. Acad. Sci. USA 104:3719–3724.

Bjorkstedt, E. P., L. K. Rosenfeld, B. A. Grantham, Y. Shkedy, and J. Roughgarden.
2002. Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. Mar. Ecol. Prog. Ser. 242:215–228.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas.
2005 Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Mar. Ecol. Prog. Ser. 298:41–57.

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller.
2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California Current. Fish. Bull. 102:25–46.

Brodeur, R. D., W. G. Pearcy, and S. Ralston.
2003. Abundance and distribution patterns of nekton and micronekton in the northern California Current transition zone. J. Oceanogr. 59:515–535.

Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips.
2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys. Res. Lett. 33, L22S08. doi:10.1029/2006GL026614.

Clarke, K. R., and R. M. Warwick.
2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed., 169 p. PRIMER-E, Plymouth, U.K.

Croll, D. A., B. Marinovic, S. Benson, F. P. Chavez, N. Black, R. Ternullo, and B. R. Tershy.
2005. From wind to whales: trophic links in a coastal upwelling system. Mar. Ecol. Prog. Ser. 289:117–130.

Davis, R. E.
1985. Drifter observations of coastal surface currents during CODE: the method and descriptive view. J. Geophys. Res. 90:4741–4755.

Ebert, T. A., and M. P. Russell.
1988. Latitudinal variation in size structure of the west coast purple sea urchin: A correlation with headlands. Limnol. Oceanogr. 33:286–294.

Emmett, R. L., G. K. Krutzikowsky, and P. Bentley.
2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog. Oceanogr. 68:1–26.

Field, J. C., R. C. Francis, and K. Aydin.
2006. Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the northern California Current. Prog. Oceanogr. 68:238–270.

Francis, R. C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston.
2007. Ten commandments for ecosystem-based fisheries scientists. Fisheries 32(5):217–233.

Fréon, P., P. Cury, L. Shannon, and C. Roy.
2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. Bull. Mar. Sci. 76:385–462.

Fulton, E. A., A. D. M. Smith, and A. E. Punt.
2005. Which ecological indicators can robustly detect effects of fishing? ICES J. Mar. Sci. 62:540–551.

Gan, J., and J. S. Allen.
2002. A modeling study of shelf circulation off northern California in the region of the Coastal Ocean Dynamics Experiment 2. Simulations and comparisons with observations. J. Geophys. Res. 107(C11), 3184, doi:10.1029/2001JC001190.

Goericke, R., E. Venrick, A. Mantyla, R. Hooff, C. Collins, G. Gaxiola-Castro, S. J. Bograd, F. B. Schwing, W. T. Peterson, B. Marinovic, R. Durazo, A. Huyer, R. L. Smith, P. A.Wheeler, F. Chavez, N. Lo, K. D. Hyrenbach, W. J. Sydeman.
2005. The state of the California Current, 2004–2005: Still cool? Calif. Coop. Ocean. Fish. Inves. Rep. 46: 32–71.

Graham, W. M., J. G. Field, and D. C. Potts.
1992. Persistent "upwelling shadows" and their influence on zooplankton distributions. Mar. Biol. 114:561–570.

Jahncke, J., B. L. Saenz, C. L. Abraham, C. Rintoul, R. W. Bradley, and W. J. Sydeman.
2008. Ecosystem responses to short-term climate variability in the Gulf of the Farallones, California. Prog. Oceanogr. 77:182–193.

Jennings, S., M. J. Kaiser, and J. D. Reynolds.
2001. Marine fisheries ecology. Blackwell Science, U.K.

Kaplan, D. M., and J. Largier.
2006. HF radar-derived origin and destination of surface waters off Bodega Bay, California. Deep-Sea Res., pt. II, 53:2906–2930.

Keister, J. E., W. T. Peterson, and S. D. Pierce.
2009. Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California Current. Deep-Sea Res., pt. I, 56:212– 231.

Largier, J. L.
2004. The importance of retention zones in the dispersal of larvae. *In* Aquatic protected areas as fisheries management tools, vol. 42 (J. B. Shipley, ed.), p. 105–122. Am. Fish. Soc., Bethesda, MD.

Largier, J. L., C. A. Lawrence, M. Roughan, D. M. Kaplan, E. P. Dever, C. E. Dorman, R. M. Kudela, S. M. Bollens, F. P. Wilkerson, R. C. Dugdale, L. W. Botsford, N. Garfield, B. Cervantes, and D. Koracin.
2006. WEST: a northern California study of the role of

wind-driven transport in the productivity of coastal plankton communities. Deep-Sea Res., pt. II 53:2833–2849.

Levin, P. S., M. J. Fogarty, S. A. Murawski, and D. Fluharty.
2009. Integrated Ecosystem Assessments: Developing the scientific basis for ecosystem-based management of the ocean. PLoS Biology 7(1) e1000014:0023–0028.

Link, J. S., J. K. T. Brodziak, S. F. Edwards, W. J. Overholtz, D. Mountain, J. W. Jossi, T. D. Smith, and M. J. Fogarty.
2002. Marine ecosystem assessment in a fisheries management context. Can. J. Fish. Aquat. Sci. 59:1429–1440.

Litz, M. N. C., S. S. Heppell, R. L. Emmett, and R. D. Brodeur.
2008. Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. west coast. Calif. Coop. Ocean. Fish. Inves. Rep. 49:167–182.

MacCall, A.
2009. A short scientific history of the fisheries. *In* Climate change and small pelagic fish (D. Checkley, J. Alheit, Y. Oozeki, and C. Roy, eds.), p. 6–11. Cambridge Univ. Press, U.K.

Mace, A. J., and S. G. Morgan.
2006. Larval accumulation in the lee of a small headland: implications for the design of marine reserves. Mar. Ecol. Prog. Ser. 318:19–29.

MacFarlane, R. B.
2010. Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can. J. Fish. Aquat. Sci. 67:1549–1565.

MacFarlane, R. B., S. Ralston, C. Royer, and E. C. Norton.
2005. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth on the central California coast during the 1998 El Niño and 1999 La Niña. Fish. Oceanogr. 14:321–332.

Mais, K. F.
1974. Pelagic fish surveys in the California Current. Cal. Fish. Bull. 162:1–79.

Morgan, C. A., W. T. Peterson, and R. L. Emmett.
2003. Onshore-offshore variations in copepod community structure off the Oregon coast during the summer upwelling season. Mar. Ecol. Prog. Ser. 249:223–236.

Nelson, C. S.
1977. Wind stress and wind stress curl over the California Current. NOAA Tech. Rep. NMFS- SSRF-714, 87 p.

Olson, D. B., G. L. Hitchcock, A. J. Mariano, C. J. Ashjian, G. Peng, R. W. Nero, and G. P. Podesta.
1994. Life on the edge: Marine life and fronts. Oceanography 7:52–60.

Orsi, J. A., J. A. Harding, S. S. Pool, R. D. Brodeur, L. J. Haldorson, J. M. Murphy, J. H. Moss, E. V. J. Farley, R. M. Sweeting, J. F. T. Morris, M. Trudel, R. J. Beamish, R. L. Emmett, and E. A. Fergusson.
2007. Epipelagic fish assemblages associated with juvenile pacific salmon in neritic waters of the California Current and the Alaska current. *In* The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons, vol. 57 (C. B. Grimes, R. D. Brodeur, L. J. Haldorson, and S. M. McKinnell, eds.), p. 105–155. Am. Fish. Soc, Bethesda, MD.

Paduan, J. D., and L. K. Rosenfeld.
1996. Remotely sensed surface currents in Monterey Bay from shore-based HF radar (Coastal Ocean Dynamics Application Radar). J. Geophys. Res. 101:20669–20686.

Parnel, M. M., R. L. Emmett, and R. D. Brodeur.
2008. Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish. Bull. 106:161–173.

Parrish, R. H., A. Bakun, D. M. Husby, and C. S. Nelson.
1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. FAO Fish. Rep. 291(3):731–778.

Peterson, W. T., R. Emmett, R. Goericke, E. Venrick, A. Mantyla, S. J. Bograd, F. B. Schwing, R. Hewitt, N. Lo, W. Watson, J. Barlow, M. Lowry, S. Ralston, K. A. Forney, B. E. Lavaniegos, W. J. Sydeman, D. Hyrenbach, R. W. Bradley, P. Warzybok, F. Chavez, K. Hunter, S. Benson, M. Weise, J. Harvey, G. Gaxiola-Castro, R. Durazo.
2006. The state of the California Current, 2005–2006: Warm in the north, cool in the south. Calif. Coop. Ocean. Fish. Invest. Rep. 47:30–74.

Peterson, W. T., and C. B. Miller.
1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull. 75:717–724.

Rebstock, G. A.
2003. Long-term change and stability in the California Current system: lessons from CalCOFI and other long-term data sets. Deep-Sea Res., pt. II, 50:2583–2594.

Reese, D. C., and R. D. Brodeur.
2006. Identifying and characterizing biological hotspots in the northern California Current. Deep-Sea Res., pt. II, 53:291–314.

Rice, J. C. and M. J. Rochet.
2005. A framework for selecting a suite of indicators for fisheries management. ICES J. Mar. Sci. 62:516–527.

Roesler, C. S., and D. B. Chelton.
1987. Zooplankton variability in the California Current, 1951–1982. Calif. Coop. Ocean. Fish. Inves. Rep. 28:59–96.

Roughgarden, J., J. T. Pennington, D. Stoner, S. Alexander, and K. Miller.
1991. Collisions of upwelling fronts with the intertidal zone: The cause of recruitment pulses in barnacle populations of central California. Acta Oecol. 12:35–51.

Samhouri, J. F., P. S. Levin, and C. J. Harvey.
2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems 12:1283–1298.

Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua.
2006. Delayed coastal upwelling along the U.S. West Coast in 2005: A historical perspective. Geophys. Res. Lett. 33, L22S01. doi:10.1029/2006GL026911.

Schwing, F. B., D. M. Husby, N. Garfield, and D. E. Tracy.
1991. Mesoscale oceanic response to wind events off central California in spring 1989: CTD surveys and AVHRR imagery. Calif. Coop. Ocean. Fish. Inves. Rep. 32:47–62.

Sims, D. W., and V. A. Quayle.
1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460–464.

Steger, J. M., F. B. Schwing, C. A. Collins, L. K. Rosenfeld, N. Garfield, and E. Gezgin.
2000. The circulation and water masses in the Gulf of the Farallones. Deep-Sea Res., pt. II, 47:907–946.

Sydeman, W. J., R. W. Bradley, P. Warzybok, C. L. Abraham, J. Jahncke, K. D. Hyrenbach, V. Kousky, J. M. Hipfner, and M. D. Ohman.
2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? Geophys. Res. Lett. 33, L22S09. doi:10.1029/2006GL026736.

Vander Woude, A. J., J. L. Largier, and R. M. Kudela.
2006. Nearshore retention of upwelled waters north and south of Point Reyes (northern California) - patterns of surface temperature and chlorophyll observed in CoOP WEST. Deep-Sea Res., pt. II, 53:2985–2998.

Ware, D. M., and R. E. Thomson.
2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. Science 308:1280–1284.

Wilkerson, F. P., R. C. Dugdale, A. Marchi, and C. A. Collins.
2002. Hydrography, nutrients and chlorophyll during El Niño and La Niña 1997–99 winters in the Gulf of the Farallones, California. Prog. Oceanogr. 54:293–310.

Wing, S. R., L. W. Botsford, S. V. Ralston, and J. L. Largier.
1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol. Oceanogr. 43:1710–1721.

Appendix 1

Summary of 2000–05 trawl catch by species or broader taxa as defined in the text, averaged over all available hauls by region, year, and season. Numbers are fish abundance/10^6 m^3, not transformed. Sample size for each reporting period is given in Table 1. Haul avg.=overall average fish density (abundance/10^6 m^3) within each region from 2000 to 2005; % Total = percentage of species contribution to the total regional catch during 2000–05; % F.O.=percent frequency of species occurrence within regional hauls during 2000–05. Only species contributing ≥5% of individuals to one or more hauls in a region are shown. C-O is named for the distinctive geometric pattern seen on the tail.

			2000		2001	
Common name	Family	Species	Summer	Fall	Summer	Fall
North coast (NC)						
thresher shark	Alopiidae	*Alopias vulpinus*	...	...	...	...
wolf-eel	Anarhichadidae	*Anarrhichthys ocellatus*	...	...	...	...
sablefish	Anoplopomatidae	*Anoplopoma fimbria*	...	...	...	...
jacksmelt	Atherinidae	*Atherinopsis californiensis*	0.90	...	1.01	...
plainfin midshipman	Batrachoididae	*Porichthys notatus*	...	...	...	...
speckled sanddab	Bothidae	*Citharichthys stigmaeus*	...	...	...	...
jack mackerel	Carangidae	*Trachurus symmetricus*	...	...	...	...
blue shark	Carcharhinidae	*Prionace glauca*	1.79	...	...	...
medusafish	Centrolophidae	*Icichthys lockingtoni*	...	18.35	4.92	1.20
Pacific sardine	Clupeidae	*Sardinops sagax*	...	...	...	2.54
Pacific herring	Clupeidae	*Clupea pallasii*	...	...	...	...
Pac. staghorn sculpin	Cottidae	*Leptocottus armatus*	...	...	...	...
northern anchovy	Engraulidae	*Engraulis mordax*	...	...	...	0.28
Pacific tomcod	Gadidae	*Microgadus proximus*	...	...	...	...
lingcod	Hexagrammidae	*Ophiodon elongatus*	...	...	...	...
Pacific hake	Merlucciidae	*Merluccius productus*	...	...	...	...
ocean sunfish	Molidae	*Mola mola*	...	...	...	...
bat ray	Myliobatidae	*Myliobatis californica*	...	...	...	...
surf smelt	Osmeridae	*Hypomesus pretiosus*	...	...	...	0.28
whitebait smelt	Osmeridae	*Allosmerus elongatus*	...	...	...	...
smelt, unidentified	Osmeridae	smelt, unidentified	...	...	...	...
C-O turbot	Pleuronectidae	*Pleuronichthys coenosus*	...	...	...	...
starry flounder	Pleuronectidae	*Platichthys stellatus*	...	...	...	...
longnose skate	Rajidae	*Raja rhina*	...	...	...	...
Chinook salmon, jv	Salmonidae	*Oncorhynchus tshawytscha*	2.69	3.13	5.04	3.22
Chinook salmon, ad	Salmonidae	*Oncorhynchus tshawytscha*	...	...	...	0.91
coho salmon	Salmonidae	*Oncorhynchus kisutch*	...	...	...	...
steelhead	Salmonidae	*Oncorhynchus mykiss*	...	...	...	...
white seabass	Sciaenidae	*Atractoscion nobilis*	...	...	...	...
Pacific saury	Scomberesocidae	*Cololabis saira*	...	60.39	...	...
Pacific mackerel	Scombridae	*Scomber japonicus*	...	...	...	...
rockfish, unidentified	Scorpaenidae	rockfish, unidentified	...	...	...	...
squarespot rockfish	Scorpaenidae	*Sebastes hopkinsi*	...	...	...	...
shortbelly rockfish	Scorpaenidae	*Sebastes jordani*	...	...	...	...
spiny dogfish shark	Squalidae	*Squalus acanthias*	...	...	...	...
Pacific butterfish	Stromateidae	*Peprilus simillimus*	...	1.27	2.02	...
Pacific electric ray	Torpedinidae	*Torpedo californica*	...	...	...	...
king-of-the-salmon	Trachipteridae	*Trachipterus altivelis*	...	...	...	...
flatfish, unidentified		flatfish, unidentified	...	...	...	...

2002		2003		2004		2005		NC		
Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Haul avg.	% Total	% F.O.
...	...	...	0.03	...	...	...	...	0.00	0.00	0.8
...	0.25	...	...	0.29	...	0.27	...	0.11	0.07	10.7
...	...	...	...	4.25	...	...	...	0.55	0.36	3.1
...	0.21	...	1.78	266.53	27.08	63.02	65.62	59.21	39.16	48.1
...	...	...	...	...	0.04	0.05	...	0.01	0.01	1.5
...	0.27	...	...	...	...	...	...	0.02	0.02	0.8
...	...	...	...	8.78	1.61	1.18	...	1.61	1.07	15.3
...	...	...	...	0.04	0.06	...	...	0.03	0.02	3.1
0.92	4.76	...	4.33	0.11	1.62	...	0.29	1.59	1.05	29.8
...	...	...	1.23	...	5.26	0.17	4.93	1.75	1.16	21.4
...	1.70	0.08	...	1.88	0.04	322.59	0.09	59.51	39.36	18.3
...	...	...	...	0.05	...	...	...	0.01	0.00	0.8
...	...	...	0.29	0.11	7.00	0.08	62.27	9.27	6.13	16.0
...	2.45	0.15	...	0.17	1.77	...	...	0.52	0.35	12.2
14.69	...	0.14	...	0.04	...	...	...	0.69	0.46	3.8
0.43	...	...	...	0.04	...	0.03	...	0.03	0.02	2.3
...	...	...	...	0.97	0.13	...	...	0.15	0.10	8.4
...	...	...	...	0.04	0.05	...	0.04	0.02	0.01	2.3
...	4.64	...	...	22.95	0.07	...	0.05	3.40	2.25	6.1
...	...	...	...	...	...	0.05	...	0.01	0.01	0.8
...	...	...	...	...	...	0.05	...	0.01	0.01	0.8
...	...	...	...	...	0.03	...	...	0.01	0.00	0.8
...	...	...	...	...	...	0.05	...	0.01	0.01	0.8
...	...	...	...	...	0.04	...	...	0.01	0.00	0.8
...	5.88	3.38	0.92	25.93	1.90	14.37	3.56	7.93	5.24	60.3
...	0.09	0.94	...	4.37	0.07	2.07	1.15	1.23	0.82	33.6
...	...	0.23	...	...	...	0.37	...	0.09	0.06	4.6
...	...	...	...	0.16	...	0.09	...	0.04	0.02	3.8
...	...	...	...	...	...	0.05	...	0.01	0.01	0.8
...	...	...	13.51	...	1.36	0.15	0.28	2.54	1.68	7.6
...	...	...	...	...	...	...	0.09	0.01	0.01	1.5
6.81	...	...	0.06	...	...	...	0.05	0.32	0.21	4.6
...	...	...	...	...	...	0.03	...	0.01	0.00	0.8
...	...	...	...	...	0.03	...	...	0.01	0.00	0.8
...	...	...	...	...	...	0.36	...	0.07	0.04	0.8
0.22	...	...	...	...	...	...	1.60	0.27	0.18	6.9
...	...	...	...	...	...	0.10	...	0.02	0.01	1.5
...	...	0.08	...	...	...	...	...	0.01	0.00	0.8
...	0.54	...	0.41	...	...	0.03	0.09	0.10	0.07	3.8

continued

Appendix 1 (continued)

Common name	Family	Species	2000 Summer	2000 Fall	2001 Summer	2001 Fall
Gulf of the Farallones (GF)						
thresher shark	Alopiidae	*Alopias vulpinus*	...	...	...	...
wolf-eel	Anarhichadidae	*Anarrhichthys ocellatus*	...	...	0.50	...
jacksmelt	Atherinidae	*Atherinopsis californiensis*	...	0.54	23.86	4.66
California grunion	Atherinidae	*Leuresthes tenuis*	...	...	...	1.24
plainfin midshipman	Batrachoididae	*Porichthys notatus*	...	...	...	...
Pacific sanddab	Bothidae	*Citharichthys sordidus*	0.23	...	...	...
jack mackerel	Carangidae	*Trachurus symmetricus*	...	...	...	...
medusafish	Centrolophidae	*Icichthys lockingtoni*	0.36	5.32	7.61	0.63
Pacific herring	Clupeidae	*Clupea pallasii*	757.09	3381.56	422.49	38.58
Pacific sardine	Clupeidae	*Sardinops sagax*	...	0.18	3.46	0.40
American shad	Clupeidae	*Alosa sapidissima*	...	...	...	0.25
Pac. staghorn sculpin	Cottidae	*Leptocottus armatus*	0.29	...	...	...
shiner surfperch	Embiotocidae	*Cymatogaster aggregata*	...	1.14	...	0.29
northern anchovy	Engraulidae	*Engraulis mordax*	0.91	90.97	...	8.41
Pacific tomcod	Gadidae	*Microgadus proximus*	...	...	4.56	0.88
threespine stickleback	Gasterosteidae	*Gasterosteus aculeatus*	...	...	...	...
lingcod	Hexagrammidae	*Ophiodon elongatus*	...	...	...	...
ragfish	Icosteidae	*Icosteus aenigmaticus*	...	...	...	...
Pacific hake	Merlucciidae	*Merluccius productus*	...	...	...	...
ocean sunfish	Molidae	*Mola mola*	...	0.18	...	...
bat ray	Myliobatidae	*Myliobatis californica*	...	...	...	...
whitebait smelt	Osmeridae	*Allosmerus elongatus*	367.78	...	...	2.18
smelt, unidentified	Osmeridae	smelt, unidentified	...	...	1.44	141.28
surf smelt	Osmeridae	*Hypomesus pretiosus*	...	...	...	...
longfin smelt	Osmeridae	*Spirinchus thaleichthys*	1.59	...	0.16	...
night smelt	Osmeridae	*Spirinchus starksi*	...	...	...	...
English sole	Pleuronectidae	*Parophrys vetulus*	...	...	...	...
big skate	Rajidae	*Raja binoculata*	0.58	...	...	...
Chinook salmon jv	Salmonidae	*Oncorhynchus tshawytscha*	15.71	1.32	5.52	0.84
Chinook salmon ad	Salmonidae	*Oncorhynchus tshawytscha*	0.29	...	0.52	0.29
white croaker	Sciaenidae	*Genyonemus lineatus*	13.14	...	...	3.47
Pacific saury	Scomberesocidae	*Cololabis saira*	...	4.17	...	...
Pacific mackerel	Scombridae	*Scomber japonicus*	1.44	...	...	...
rockfish, unidentified	Scorpaenidae	rockfish, unidentified	...	...	0.38	...
yellowtail rockfish	Scorpaenidae	*Sebastes flavidus*	...	...	...	...
blue rockfish	Scorpaenidae	*Sebastes mystinus*	...	...	...	...
California barracuda	Sphyraenidae	*Sphyraena argentea*	...	...	...	...
spiny dogfish shark	Squalidae	*Squalus acanthias*	0.29	...	...	...
Pacific butterfish	Stromateidae	*Peprilus simillimus*	...	2.15	0.54	0.59
Pacific electric ray	Torpedinidae	*Torpedo californica*	...	...	0.32	...
flatfish, unidentified		flatfish, unidentified	...	...	...	...

2002		2003		2004		2005		GF		
Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Haul avg.	% Total	% F.O.
...	...	...	0.07	...	...	...	...	0.01	0.00	1.1
0.37	0.35	0.15	0.37	0.20	...	0.31	...	0.21	0.01	13.8
0.42	12.53	4.56	...	1.50	1169.64	380.09	120.75	117.81	4.31	33.3
...	...	...	...	...	...	...	...	0.07	0.00	1.1
0.12	...	...	0.08	...	...	...	...	0.02	0.00	2.3
...	...	...	...	...	...	5.21	0.15	0.38	0.01	3.4
...	...	...	0.30	...	4.32	...	0.15	0.34	0.01	5.7
0.38	1.37	...	4.32	1.89	2.92	...	...	2.20	0.08	31.0
4884.23	40.74	1162.64	330.65	60.84	...	1311.41	176.41	1215.61	44.48	43.7
4.94	...	151.11	10.15	829.45	28.50	65.38	2.90	98.86	3.62	26.4
2.77	...	0.71	...	0.11	...	...	...	0.41	0.01	6.9
...	...	...	...	...	...	...	...	0.02	0.00	1.1
...	...	...	0.18	...	...	...	...	0.14	0.01	3.4
1076.73	1.41	0.14	61.39	0.87	1.45	14450.22	1439.88	1219.37	44.62	28.7
0.22	0.35	8.07	2.07	37.82	...	0.19	...	4.94	0.18	25.3
0.84	...	...	...	...	...	...	...	0.10	0.00	1.1
0.12	...	0.09	...	...	...	...	...	0.02	0.00	2.3
...	...	...	...	0.43	...	...	...	0.04	0.00	1.1
3.52	...	...	...	...	...	...	...	0.41	0.01	1.1
...	0.11	...	...	1.01	...	...	0.15	0.13	0.00	6.9
...	...	...	...	0.20	0.12	...	...	0.03	0.00	3.4
1.05	16.65	214.01	8.70	...	...	4.26	...	48.11	1.76	20.7
...	0.46	...	1.45	...	...	0.76	...	8.50	0.31	9.2
30.68	...	...	...	...	0.12	...	...	3.53	0.13	3.4
0.22	...	...	...	...	...	...	...	0.15	0.01	3.4
...	...	...	0.25	...	...	...	...	0.03	0.00	1.1
...	0.09	...	...	...	...	...	...	0.01	0.00	1.1
...	...	...	...	...	...	...	...	0.04	0.00	1.1
13.56	3.46	8.43	0.75	3.35	0.51	10.65	4.45	5.77	0.21	55.2
2.10	0.67	1.03	0.09	3.42	0.32	5.22	0.21	1.19	0.04	32.2
0.57	...	...	...	...	...	...	...	1.17	0.04	5.7
...	...	...	0.10	...	...	...	...	0.40	0.01	2.3
...	...	...	...	...	...	...	0.31	0.12	0.00	2.3
...	...	...	...	...	...	...	...	0.03	0.00	1.1
3.36	...	...	...	...	...	...	...	0.39	0.01	1.1
1.26	...	...	...	...	...	...	...	0.14	0.01	1.1
...	0.23	...	...	...	...	...	...	0.02	0.00	1.1
...	...	...	...	...	...	...	...	0.02	0.00	1.1
1.82	0.12	...	0.84	0.10	...	8.22	14.47	2.00	0.07	20.7
...	...	0.14	0.40	0.28	0.12	...	...	0.12	0.00	8.0
...	1.31	...	...	...	...	0.81	...	0.18	0.01	2.3

The effects of temperature on hatching and survival of northern rock sole larvae (*Lepidopsetta polyxystra*)

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Abstract—Northern rock sole (*Lepidopsetta polyxystra*) is a commercially important flatfish in Alaska and was recently classified as a distinct species from southern rock sole (*L. bilineata*). Taxonomic and vital rate data for northern rock sole are still not fully described, notably at early egg and larval stages. In this study, we provide new taxonomic descriptions of late-stage eggs and newly hatched larvae, as well as temperature-response models of hatching (timing, duration, success), and larval size-at-hatch and posthatch survival at four temperatures (2°, 5°, 9°, and 12°C). Time-to-first-hatch, hatch cycle duration, and overall hatching success showed a negative relationship with temperature. Early hatching larvae within each temperature treatment were smaller and had larger yolk sacs, but larvae incubated at higher temperatures (9° and 12°C) had the largest yolk reserves overall. Despite having smaller yolks, size-at-hatch and the maximum size achieved during the hatching cycle was highest for larvae reared at cold temperatures (2° and 5°C), indicating that endogenous reserves are more efficiently used for growth at these temperatures. In addition, larvae reared at high temperatures died more rapidly in the absence of food despite having more yolk reserves than cold-incubated larvae. Overall, northern rock sole eggs and larvae display early life history traits consistent with cold-water adaptation for winter spawning in the North Pacific.

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Temperature is arguably the most important environmental influence driving development, growth, and survival of marine fish during their early life history (Pepin, 1991). In cold water marine systems, small fluctuations in temperature can have profound effects on an individual's vital rates, which at the population level can mediate connectivity patterns (Laurel and Bradbury, 2006; O'Connor et al., 2007), genetic structure (Bradbury et al., 2010), cohort survival, and eventual recruitment to the adult fish population (Houde, 2008). However, beyond the general positive relationships between temperature and poikilothermic metabolism (Jobling, 1997), the temperature response for fish is highly variable among species and populations, necessitating the measurement of temperature effects on a species-by-species basis. In commercially harvested species, this information is useful for estimating spawning stock biomass (using daily egg production methods; DEPM; Pena et al., 2010), measuring larval mortality (Pepin, 1991), and predicting recruitment (Houde, 2008).

Northern rock sole (*Lepidopsetta polyxystra*) is a commercially harvested marine fish in Alaskan waters and was recently classified as a distinct species from southern rock sole (*L. bilineata*) (Orr and Matarese, 2000). Northern rock sole spawn earlier in the year (mid-winter) compared to southern rock sole (summer) in the region around Kodiak Island (Stark and Somerton, 2002). Pertseva-Ostroumova (1961) reported peak spawning of northern rock sole (as *Lepidopsetta bilineata bilineata*) off the east coast of Kamchatka from late March to early April and described egg and larval development at temperatures averaging 2.9–3.5°C. However, temperature effects on growth, mortality, and behavior have been principally restricted to the postsettlement phase (Hurst and Duffy, 2005; Laurel et al., 2007; Hurst et al., 2010). The egg and larval phases of eastern Bering Sea and Gulf of Alaska northern rock sole remain poorly understood, with the exception of descriptive studies on the taxonomy and distribution of *Lepidopsetta* spp. (Matarese et al., 1989, 2003; Orr and Matarese, 2000; Lanksbury et al., 2007).

The Gulf of Alaska and Bering Sea are experiencing extensive changes in environmental conditions, which in turn have affected seasonal temperature, ice extent, and larval prey production (Hunt et al., 2002). These changes raise concerns on how northern rock sole will respond directly to such environments. Developmental

data for northern rock sole are available for stocks in the western Bering Sea (Pertseva-Ostroumova, 1961), but these data, in addition to not being geographically representative of Alaskan waters, are incomplete to develop a full temperature-development model. Descriptions of late-stage eggs and newly hatched larvae are also absent for northern rock sole larvae in Alaskan waters despite their commercial importance. Therefore, the objectives of this study were 1) to provide a description of late-stage eggs and newly hatched northern rock sole larvae from laboratory reared specimens, and 2) to measure and model temperature effects on development rate, survival, and morphometric features (e.g., hatch length, condition, yolk volume) of eggs and newly hatched northern rock sole larvae from the eastern Pacific Ocean (Gulf of Alaska).

Materials and methods

Broodstock collections

Adult northern rock sole (n=25; 32–40 cm total length [TL]) were collected at 30-m depth by trawl vessels in Chiniak Bay, Kodiak, AK (57°46′N, 152°21′W) during late August in 2009. Adults were transported to shore and held without food for a 48-hour period at the Kodiak Fisheries Research Center (KFRC) to prepare them for shipment to the Hatfield Marine Science Center (HMSC) in Newport, OR. Fish were placed in 10-L plastic bags filled with <500 mL of filtered seawater and saturated with pure oxygen, and then packed into chilled coolers for 24 hours during transport to the HMSC. Upon arrival, northern rock sole were transferred to a 3-m round holding tank with sand substrate and held under a temperature and photoperiod schedule simulating conditions in Chiniak Bay. Fish were fed a gelatinized combination of herring, capelin, and squid three times weekly during the holding period.

Males and females showed signs of sexual maturation starting in February that were similar to reported maturity schedules for adults sampled near our collection sites (Stark and Somerton, 2002). Mature males and females were injected with a luteinizing-hormone-releasing hormone (LNHRa) and strip-spawned 24 hours later by gentle squeezing of the abdomen. The gametes of ripe males (n=3) and a female (n=1) were combined in a clean, dry container for a 1-minute period before the addition of ambient seawater. Seawater was added repeatedly and decanted from the egg batches to rinse away excess milt and tissue.

The use of a single female and multiple males did not rule out possible parental contributions to eggs that would affect survival between different batches of eggs (*sensu* Chambers et al., 1989). However, our goal was not to determine the range of variation in egg characteristics. Rather, the experiment was designed to isolate the effects of temperature on the vital rates of eggs and larvae. Fertilized eggs were held for a 6-hour period at 4°C and gradually adjusted over 24 hours to temperature treatments of the experimental apparatus to initiate the experiments.

Egg incubation

The rearing of northern rock sole eggs was conducted in a temperature-controlled, flow-through system consisting of four temperature treatments: 2°, 5°, 9°, and 12°C. Temperature-adjusted seawater was fed to a series of seawater baths (i.e., 1×1×0.5 m square tanks): four replicates of temperature treatments at 2°, 5°, and 9°C and three replicates at 12°C; n=15 total tanks. Temperature-controlled seawater was supplied to each of the seawater baths at a rate of 2–3 L/min. A 4-L plastic egg incubation basket with 220-µm mesh sides and solid bottom was placed within each temperature bath. Eggs were scattered in a thin layer over the bottom of each basket (2 mL of eggs per basket). Based on counts from 2-mL egg volumes (n=5), the number of eggs equaled 1701 ±42 eggs (mean ±1 standard deviation [SD]) per egg basket. An air stone was placed in each basket to increase water flow over eggs during the incubation period. In addition to the egg baskets, water baths were outfitted with 1-L mesh-bottomed containers to hold newly hatched larvae for observation beyond the hatching period. Gently lifting and lowering containers in the seawater bath twice daily achieved seawater exchange within each container. Before hatch, 50 eggs were preserved in a 5% buffered formalin solution, and measured to the nearest 0.01 mm with a dissecting microscope with transmitted light. All taxonomic descriptions egg and larval stages were based upon individual samples from the 2°C treatment.

Experimental design

Egg baskets were checked daily during the course of the experiment for any signs of hatch. At the onset of hatch, larvae were counted daily and removed from the basket, a subsample of which was taken for morphometric measurements (n=10–18 larvae). However, to quantify "hatch quality," all removed larvae were inspected for malformations (i.e., curved or twisted shape) before being discarded. Subsampled larvae were anesthetized with a 0.0005 ppm solution of tricane methanesulfonate (MS-222) for measurement under a dissecting microscope. The following morphometric measurements were recorded: 1) standard length (SL); 2) myotome height at the anus (MH); 3) eye diameter (ED); and 4) yolk area. Precise length measurements (to the nearest 0.01 mm) were obtained with an image analysis system (Image-Pro Plus, Media Cybernetics, Bethesda, MD) connected to the microscope. Yolk area was determined by using the tracing tools of the image analysis software.

To determine mortality rates of unfed larvae, 100 larvae were transferred by pipette from each replicate egg basket into a corresponding 1-L plastic container with mesh bottom. Each 1-L container was suspended in a water bath, the temperature of which corresponded with that of the incubation baskets. This was done 1–2 days after the beginning of the hatch cycle to ensure

sufficient larvae were available for the containers and morphometric measurements. Daily mortality was measured by counting and removing dead larvae from each container bottom with a pipette.

Data analysis

The general linear model (GLM) was used to determine statistical differences in size (SL, mm), yolk area (YA, mm^2) and body depth (BD, mm) as a function of temperature and hatch rank. Hatch rank (HR) was calculated for each temperature treatment by dividing the hatching day by the total number of hatching days observed at that temperature. All analyses were performed on tank averages and residuals were checked to ensure the data met the assumptions of normality of the GLM. Data were plotted in three dimensions to capture the nature of significant trends and interactions.

Hatch characteristics (days to first hatch, hatch cycle duration, days to peak hatch, hatch quality, and hatch success), posthatch survival (i.e., time 50% mortality [M_{50}]) and maximum size achieved by yolksac larvae (S_{max}) were all analyzed by using linear and nonlinear regression tools in SigmaPlot, vers. 10.1(Systat Software, Inc., San Jose, CA). Model types (e.g., exponential, Gaussian, etc.) were initially selected on the basis of equivalent temperature relationships between eggs and larvae of other cold-water marine fish species (Jordaan and Kling, 2003; Laurel et al., 2008). The number of parameters in the statistical models were then chosen by using the Akaike information criterion (AIC; Akaike, 1974). The AIC value provides a relative goodness-of-fit to a range of models but penalizes models that use additional parameters to explain small amounts of variance. Models were ultimately selected if the correlation coefficient (R^2) values were greater than 90% and their AIC values were within 2 of the minimum in the range of compared models. All model fits were performed on raw data.

Results

Taxonomic description of eggs and newly hatched larvae

Egg development from fertilization to middle-late stage (tail 1¼–1½ of the way around the yolk) has been described by Pertseva-Ostroumova (1961). Late-stage eggs from our study are 0.96–1.10 mm in diameter and overlap with reported egg sizes for the genus *Lepidopsetta* (0.86–1.08 mm; Orr and Matarese 2000). Just before hatching, the tail of the embryo is 1¾ of the way around the yolk and the tail tip is even with the posterior margin of the eye. Pigment on the head is restricted to the snout, extending from just below the nares to the midbrain (Fig. 1A). The eyes are partially pigmented; a patch of larger melanophores is present on the anterodorsal quadrant and smaller fine melanophores are scattered over the dorsal half of the eye and concentrated along the upper rim of the lens (Fig. 1B).

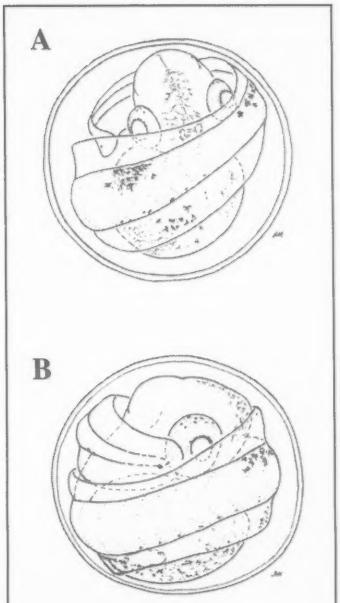

Figure 1

Illustrations of (**A**) front view, and (**B**) side view of a late-stage northern rock sole (*Lepidopsetta polyxystra*) egg measuring 1.02 mm diameter (32 days after fertilization at 2°C). Illustrations by A. Maust, National Marine Fisheries Service, Alaska Fisheries Science Center.

Dendritic pigment is present along the posterior dorsal gut margin, vent margin, and on the ventral yolk sac. A dorsal patch of pigment is located at 50% body length (BL) and a band of pigment is present at 75% BL; below both the patch and band is corresponding pigment on the anal fin. A row of postanal ventral melanophores (PVMs) extends from the anus to the band at 75% BL. A small group of spots is present on the ventral body margin near the last 2 or 3 myomeres and an additional 3 or 4 spots are located along the ventral margin of the notochord beyond the last myomere. The most posterior spot is near the end of the notochord.

Newly hatched larvae (Fig. 2) have light dendritic pigment on the snout from the midbrain to the edge of the lower jaw. Pigment outlines the lower jaw, which is not yet open. Eyes are moderately pigmented; pigment around the lens, in the dorsoanterior quadrant, and at the posterior edge of the eye is darker. The lower lateral and ventral yolk sac is lightly pigmented with dendritic melanophores. The same type of pigment is present on the posterior edge of the yolk sac and on the dorsal area of the hindgut close to the body. A

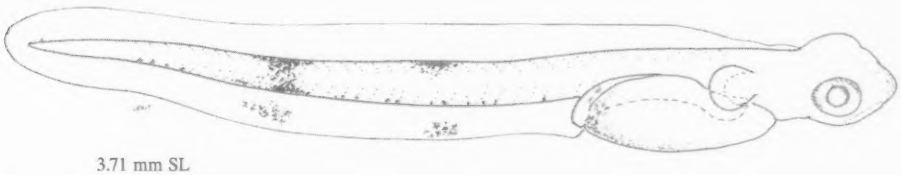

Figure 2

Newly hatched larva (day 0) of northern rock sole (*Lepidopsetta polyxystra*) SL=3.71 mm. Illustrations by A. Maust, National Marine Fisheries Service, Alaska Fisheries Science Center.

pigment patch on the dorsal half of the body is at 50% SL and a band is present at 75% SL. Below the patch and band are corresponding patches of pigment just above the ventral edge of the anal fin; anterior anal-fin pigment spots are more closely spaced than those within the posterior patch. A single row of PVMs is present starting at three myomeres posterior to the anus. These PVMs are spaced at approximately one per myomere and stop just beyond the pigment band at 75% SL. There are 4 or 5 PVMs along the last 3 or 4 myomeres. Pigment may be present on the notochord and is variable; there may be 1 or 2 spots on the ventral margin, 1 spot on the dorsal margin near the tip of the notochord, pigment only on the upper or lower margin, or no pigment may be present. Overall, northern rock sole larvae have less pigment on the postanal portion of the body than southern rock sole and can easily be differentiated. Southern rock sole larvae have an additional dorsal pigment patch 1–5 myomeres after the anus and a dorsal patch or caudal bar at the posteriormost myomere. Subsequent descriptions of preflexion, flexion, and postflexion stages of both rock sole species are found in Orr and Matarese (2000).

Hatching patterns

Successful hatching was observed in all of the temperature treatments, but hatch patterns (time to first hatch, peak hatch, and hatch duration) were negatively related to temperature as indicated in the series of exponential decay, two-parameter models shown in Figure 3 (see Table 1 for model parameter estimates). Hatch quality and hatching success were also negatively associated with temperature (Fig. 4; Table 1), largely driven by the high numbers of malformed larvae (>50%) observed in the 12°C treatment. Malformed larvae were alive but curved in appearance and had poor swimming capabilities shortly after hatching. A subset of malformed larvae held over the course of the hatch cycle continued to swim poorly and did not appear to straighten out during the entire yolksac period. Despite the malformation, these larvae survived approximately the same length of time in the absence of food as normally formed larvae held at the same temperature (~7 days; see below).

Size-at-hatch and yolk reserves (yolk area; [YA]) were a function of both temperature and timing in the hatch cycle. Overall, larval size-at-hatch ranged from 2.95 to 5.43 mm SL among all temperature treatments, but larvae were larger if they were late hatching or were incubated in colder water (Fig. 5). The maximum size-at-hatch achieved over the course of the hatch cycle occurred at 5°C (Fig. 6) and was best described by a Gaussian model (Table 1). However, the temperature effect was more apparent in late-hatching larvae as indicated by the significant interaction term (Table 2).

Yolk area also significantly varied as a function of temperature and hatch timing (Fig. 7), although the patterns were more variable than hatch size and there was no significant interaction between the two model terms (Table 2). Yolk reserves were larger in the early part of the hatch cycle and at warm incubation temperatures. However, although not statistically described in the model, larvae hatching on the second day of the hatch cycle in the 12°C treatment had larger yolk reserves than those hatching on day 1. In all other temperature treatments, larvae hatching on successive days had reduced yolk reserves.

Eye diameter varied between 0.22 and 0.33 mm and did not vary as a function of temperature or hatch rank (Table 2). However, larvae tended to have larger eyes later in the hatch cycle across all temperatures, although this was not statistically significant (P=0.066). Larger and late-hatching larvae also appeared to have more eye pigmentation than small, early-hatching larvae.

The posthatch survival time of larvae was negatively temperature dependent (Fig. 8), ranging from 12 to 34 days among temperature treatments. Survival patterns followed a type-III functional response for each temperature treatment, and there was little variability among replicates. Plots of M_{50} (point of 50% mortality) with temperature were described with an exponential decay model with an R^2=0.99 (Table 1).

Table 1

Types of models and estimated parameters for hatching patterns and posthatch survival of northern rock sole (*Lepidopsetta polyxystra*) larvae as a function of temperature (2°, 5°, 9°, and 12°C). Analysis was performed on tank means (n=3–4 tanks per temperature) of 15–20 larvae for each tank during each sampling period (n=4–10 sampling periods). Criteria for model selection are found in the *Material and Methods* section. R^2=correlation coefficient.

Variable	Model type	Equation and parameters	df	F	R^2	P
Days to first hatch	Exponential decay	$f(x)=37.516e^{-0.133x}$	1	353.010	0.97	<0.001
Hatch duration	Exponential decay	$f(x)=17.556e^{-0.119x}$	1	451.941	0.97	<0.001
Days to peak hatch	Exponential decay	$f(x)=46.499e^{-0.136x}$	1	593.968	0.98	<0.001
Hatch quality	Gaussian	$f(x)=104.872e^{-0.5\left(\frac{x-4.366}{6.023}\right)^2}$	2	55.873	0.90	<0.001
Hatch success	Gaussian	$f(x)=72.454e^{-0.5\left(\frac{x-2.194}{6.313}\right)^2}$	2	10.587	0.66	0.003
50% mortality (M_{50})	Exponential decay	$f(x)=9.951+39.970e^{-0.391x}$	2	747.608	0.99	<0.001
Maximum size-at-hatch	Gaussian	$f(x)=4.377+0.826e^{-0.5\left(\frac{x-3.782}{3.916}\right)^2}$	3	29.336	0.89	<0.001

Discussion

The temperature effects on hatching patterns (i.e., time to first hatch, hatch duration, and time to peak hatch) followed an expected negative relationship. Development rates among teleost fish are highly variable and largely a function of initial egg size (Pauly and Pullin, 1988), but temperature ultimately controls the development response curve within each fish species (Pepin, 1991; Jobling, 1997). Hatch synchrony in fish generally decreases with temperature (e.g., Ims, 1990), although it can be dependent to some extent on other environmental variables (e.g., predation; Bradbury et al., 2004). Northern rock sole appear to follow this pattern, but comparisons of our laboratory data to field data were not possible because northern rock sole eggs are demersal and have not been collected from the wild. Larvae have been captured at the surface during April–August in the Bering Sea and Gulf of Alaska when surface temperatures can vary from –1° to 10°C (Matarese et al., 2003).

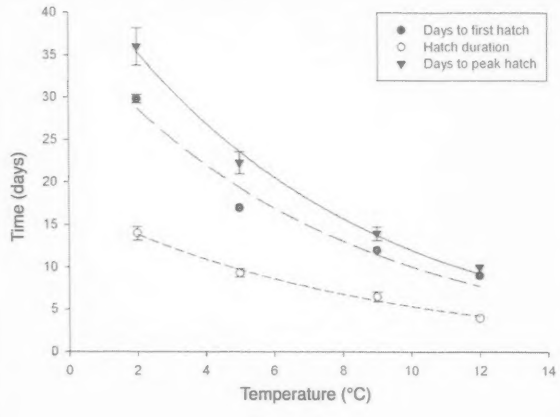

Figure 3

The effects of temperature on the number of days to first hatching (closed circles), hatch duration (open circles), and timing of peak hatching (closed triangles) in northern rock sole (*Lepidopsetta polyxystra*) eggs. Data are means (±1 standard error [SE]) based on 2 mL of eggs in three replicate tanks at each of the following temperatures: 2°, 5°, 9°, and 12°C.

Northern rock sole eggs are difficult to distinguish from co-occurring Pacific cod (*Gadus macrocephalus*) because they are similar in size (0.96–1.10 mm vs. 0.98–1.08 mm, respectively), demersal, semi-adhesive, and have a thick chorion. However, late-stage eggs of these species differ in several ways: yolk pigment is present in northern rock sole, but absent in Pacific cod, and postanal pigment on northern rock sole embryos consists of a dorsal patch at 50% SL and a band at 75% SL, whereas Pacific cod embryos have pigment bands at both 50% and 75% SL. Anal finfold pigment is present on northern rock sole embryos below the patch and band, but there is no anal finfold pigment on Pacific cod embryos.

Cold temperatures (2–5°C) produced larger larvae at time of hatching, but the effects of egg incubation temperature on hatch size in other fish species appear to be species-specific. Atlantic herring (*Clupea harengus*) and Pacific cod also produce larger larvae at low temperatures across a similar thermal range (Alderdice and Velsen, 1971; Laurel et al., 2008), whereas walleye pollock (*Theragra chalcogramma*), Atlantic silverside (*Menidia menidia)* and yellowtail flounder (*Pleuronectes ferrugineus)* tend to produce larger larvae at warmer temperatures (Bengston et al., 1987; Blood et al., 1994; Benoit and Pepin, 1999).

The effects of hatch rank (i.e., an individual's day-of-hatch within a batch of eggs) on size-at-hatch and yolk reserves have been measured in

a number of species, but the ecological significance is poorly understood. Like northern rock sole, late-hatching larvae in other marine species are generally larger and have smaller yolk sacs (e.g., capelin [*Mallotus villosus*], Chambers et al., 1989; wolffish [*Anarhichas lupus*], Ringo et al., 1987). Methven and Brown (1991) also showed similar effects on hatch rank for ocean pout (*Macrozoarces americanus*), but this pattern was only observed at low temperatures when the hatching period was extended. Alternatively, late-hatching Atlantic silverside larvae are smaller than earlier hatching larvae (Bengston et al., 1987), although this occurrence appears to be a rare exception. Interestingly, despite the increased attention on parental effects on offspring size variation in marine fish (e.g., ~1 mm size range variation [3.8–4.8 mm SL] in Atlantic cod [*Gadus morhua*] larvae, Paulsen et al. 2009), the role of hatch rank and temperature cannot be ignored because they appear to account for an equivalent (if not more) amount of variability in offspring size from a single parent (~2.5 mm size range variation [2.95–5.43 mm SL], this study).

From an evolutionary perspective, the production of offspring of variable size and yolk reserves may be a bet-hedging strategy in a variable environment of temperature, food availability, and predator risk. However, in fish larvae, the survival benefits have seldom been tested explicitly beyond a few case studies. In walleye pollock, early-hatching larvae had higher growth potential than late-hatching larvae (Porter and Bailey, 2007). Similar results have been reported for early-hatching Atlantic herring larvae (Geffen, 2002), although this effect is short-lived because early- and late-hatching Atlantic herring larvae have overlapping size-at-age and growth trajectories shortly after the onset of exogenous feeding (Panagiotaki and Geffen, 1992). In general, smaller early-hatching larvae likely have under-developed sensory organs, swim capabilities, and digestive enzymes to immediately handle feeding exogenously (Porter and Bailey, 2007). As a tradeoff, these larvae may have an extended capability for surviving in the absence of food given their larger yolk reserves (Laurel et al., 2008). The latter feature also appears to be true for northern rock sole. Although eye diameter was not significantly larger in late-hatching larvae, there was a weak trend in increased eye diameter and increased eye pigmentation to indicate increased visual development with late hatching. More importantly, as has been shown with several gadid species, yolk reserves in northern rock sole were larger in early hatching larvae. Increased yolk reserves in early-hatching Pacific cod larvae allowed individuals to live 3–8

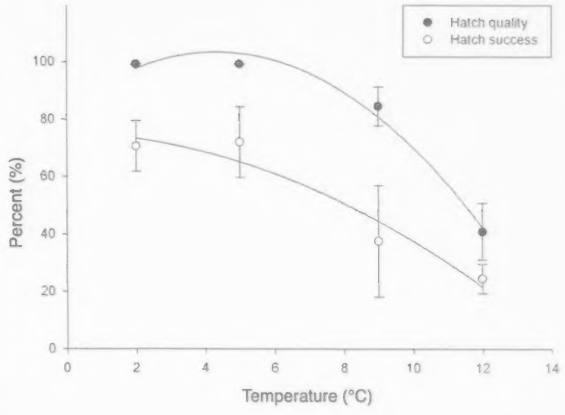

Figure 4

The effects of temperature on hatch quality (dark circles) and hatch success (open circles) of northern rock sole (*Lepidopsetta polyxystra*) eggs. Data are means (±1 standard error [SE]) based on 2 mL of eggs in three replicate tanks at each of the following temperatures: 2°, 5°, 9°, and 12°C.

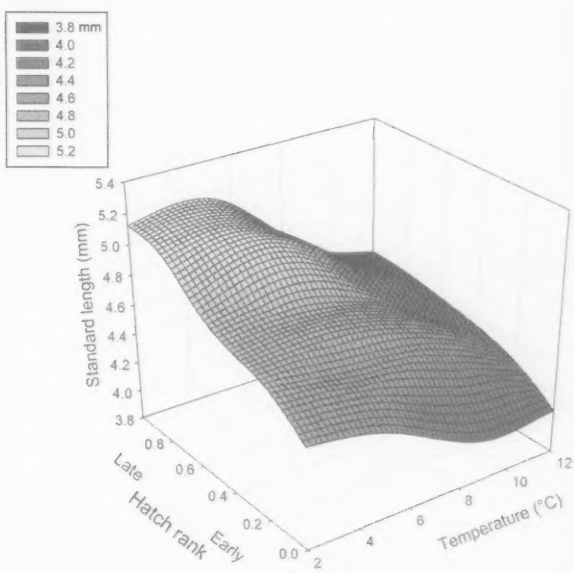

Figure 5

The effects of temperature and hatch time (days into hatch cycle) on northern rock sole (*Lepidopsetta polyxystra*) larval size-at-hatch (standard length [SL] mm). Values for SL are means (±1 standard error [SE]) based on image analysis of larvae taken from three replicate tanks (10–15 larvae sampled per tank).

Table 2

Results of the general linear model (GLM) on the effects of temperature and hatch rank on standard length (SL), yolk area (YA, mm^2) and eye diameter (ED, mm) in newly hatched northern rock sole (*Lepidopsetta polyxystra*). Analysis was performed on tank means (n=3–4 tanks per temperature) of 15–20 larvae for each tank during each sampling period (n=4–10 sampling periods).

Source	df	F	P
Standard length (SL mm)			
Temperature	1	76.26	<0.001
Hatch rank	15	25.87	<0.001
Temperature×hatch rank	1	4.08	0.048
Error	63		
Yolk area (YA mm^2)			
Temperature	1	4.49	0.038
Hatch rank	15	23.81	<0.001
Temperature×hatch rank	1	2.67	0.108
Error	63		
Eye diameter (ED mm)			
Temperature	1	0.14	0.710
Hatch rank	15	1.74	0.066
Temperature×hatch rank	1	0.56	0.457
Error	63		

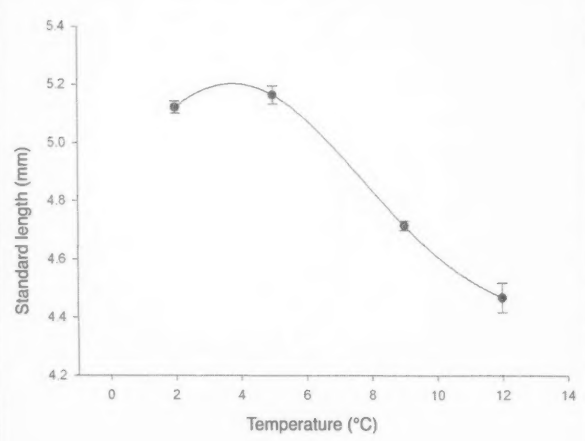

Figure 6

Maximum size-at-hatch achieved by northern rock sole (*Lepidopsetta polyxystra*) larvae as a function of temperature (2°, 5°, 9°, and 12°C). Size data are based on means (±1 standard error) of maximum size observed among replicate tanks (n=3) for each temperature of early and late-hatching larvae. Data for each hatch period were fitted with a peak, Gaussian, 4-parameter nonlinear regression shown in the figure panel.

days longer than late-hatching larvae depending on the incubation temperature (Laurel et al., 2008).

In Pacific cod, early-hatching eggs survived longer as free-swimming larvae in the absence of food than did late hatching eggs, but hatch rank had no overall effect on time-to-starvation from the point of fertilization (Laurel et al., 2008). In other words, early hatching larvae survived longer as larvae, whereas late-hatching larvae survived longer as eggs. Early hatching larvae may gain more experience handling and ingesting prey before they need to feed, or may experience higher growth potential than late-hatching larvae (Porter and Bailey, 2007).

The upper range of thermal tolerance of northern rock sole larvae appears to be around 12°C as evidenced by the precipitous decline in hatch quality at this temperature. In the wild, northern rock sole larvae seldom experience temperatures >6°C because spawning occurs in mid-winter and early spring in Alaskan waters (Stark and Somerton, 2002). Northern rock sole adults are also generally restricted to higher latitudes, from the northern coast of Hokkaido to the Okhotsk Sea in the western North Pacific Ocean, the Bering Sea near St. Lawrence Island and south to the shelf areas of the Gulf of Alaska (Mecklenburg et al., 2002). Collections of larvae have extended as far north as the Chukchi Sea and outer shelf areas of the Bering Sea where water temperatures can be below 0°C (Matarese[1]). In contrast, southern rock sole adults are distributed further south (southeastern Bering Sea along the Alaska Peninsula and throughout the shelf areas of the Gulf of Alaska to Baja California), with the most northernmost extent (rare) being documented at around 59°N (just south of Nunivak Island). Where northern and southern rock sole overlap in Alaska, southern rock sole spawning generally occurs later in the warmer summer months (Stark and Somerton, 2002). The poor hatching performance of northern rock sole at 12°C, along with the contrasting spatial and temporal distribution of northern and southern rock sole in the field, suggest temperature tolerance may be an important environmental variable reducing gene flow between these closely related pleuronectids.

It was interesting to note that despite having larger yolks, larvae in the warm water treatments starved more quickly and were not able to mobilize yolk reserves as efficiently into growth as larvae in cold temperature treatments. The growth performance in poikilotherms is generally optimized at the lower range of the organism's thermal tolerance under low-food situations (Jobling, 1997), but there is a lack of such studies at life stages when organisms are dependent on endogenous resources. In a review of more than 100 marine fish species, Pepin (1991) found that time to starvation decreases with temperature,

[1] Matarese, A. 2010. Unpubl. data. Alaska Fisheries Science Center, Seattle, WA 98115

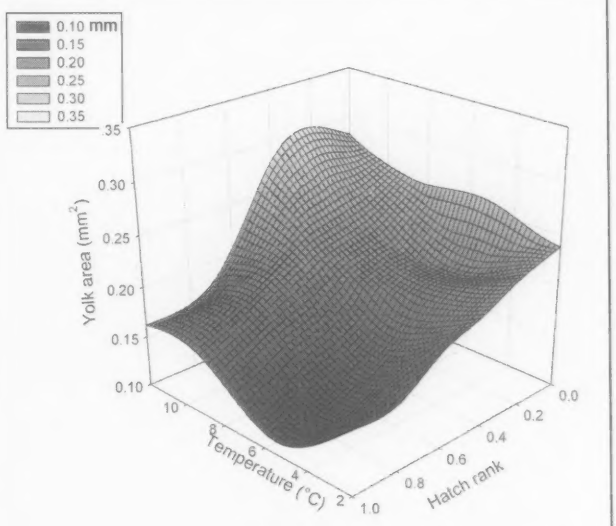

Figure 7

The effects of temperature and hatch time (days into hatch cycle) on northern rock sole (*Lepidopsetta polyxystra*) larvae yolk reserves at hatch (YA, mm²). Values for YA are means 0±1 standard error) based on image analysis of larvae taken from three replicate tanks (10–15 larvae sampled per tank).

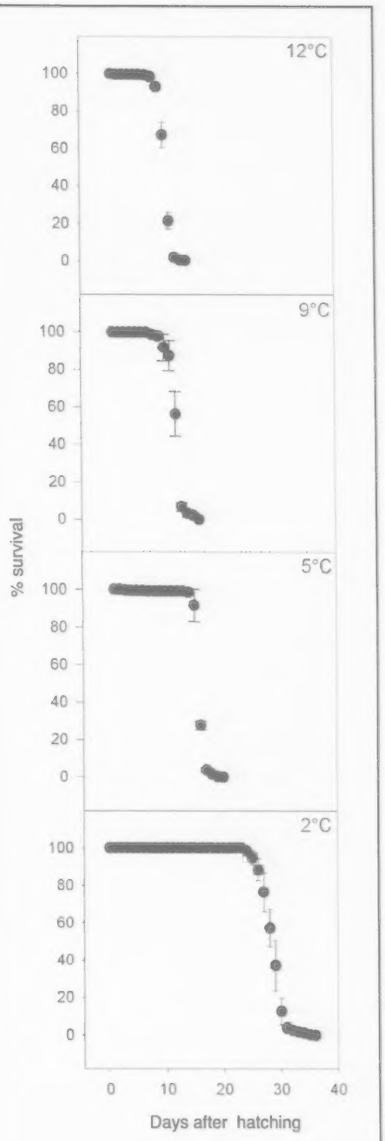

Figure 8

Time to starvation of unfed northern rock sole (*Lepidopsetta polyxystra*) larvae as a function of temperature (2°, 5°, 9°, and 12°C). Data points are means (±1 standard error) for three replicate tanks at each temperature.

but the incubation temperature, by way of mediating yolk reserves, may be an important factor in this relationship. Regardless, it appears that northern rock sole larvae have physiological adaptations to maximize the use of endogenous resources under cold conditions (i.e., ≤9°C). Similarly, the growth rates and swimming performance of juvenile northern rock sole remain relatively high at cold temperatures compared to other Alaskan flatfish species (Hurst and Abookire, 2006; Laurel et al., 2007).

Conclusion

Temperature and hatch rank had distinct effects on size-at-hatch and yolk reserves, but the effects on post-hatch survival were not fully explored. Temperature had multiple influences on northern rock sole larvae by affecting developmental rates, size-at-hatch, and metabolic demands on yolk reserves. In the absence of predators, optimal incubation temperatures for northern rock sole eggs and prefeeding larvae appear to be ~2–5°C. However, the benefits of successful hatching, increased size-at-hatching, and reduced risks of starvation need to be weighed against possible increased predation risk (e.g., stage dependent mortality; Houde, 2008) and dispersal potential (O'Connor et al., 2007) at low temperatures. In addition, it will be interesting to compare these data with those of southern rock sole, especially since differing thermal responses may be an important regulator of adult latitudinal distributions and seasonal spawning patterns between these species. Collectively, these questions will be important areas of research in the light of changing environmental conditions in the North Pacific.

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Literature cited

Akaike, H.
1974. A new look at the statistical model identification. IEEE Trans Automatic Control 19:716–723.

Alderdice, D. F., and F. P. J. Velsen.
1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Board Can. 28:1545–1562.

Bengtson, D. A., R. C. Barkman, and W. J. Berry.
1987. Relationships between maternal size, egg diameter, time of spawning season, temperature, and length at hatch of Atlantic silverside, *Menidia menidia*. J. Fish Biol. 31:697–704.

Benoit, H. P., and P. Pepin.
1999. Interaction of rearing temperature and maternal influence on egg development rates and larval size at hatch in yellowtail flounder (*Pleuronectes ferrugineus*). Can. J. Fish. Aquat. Sci. 56:785–794.

Blood, D. M., A. C. Matarese, and M. M. Yoklavich.
1994. Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 92:207–222.

Bradbury, I. R., S. E. Campana, P. Bentzen, and P. V. R. Snelgrove.
2004. Synchronized hatch and its ecological significance in rainbow smelt *Osmerus mordax* in St. Mary's Bay, Newfoundland. Limnol. Oceanogr. 49:2310–2315.

Bradbury I. R., S. Hubert, B. Higgins, T. Borza, S. Bowman, I. G. Paterson, P. V. R. Snelgrove, C. J. Morris, R. S. Gregory, D. C. Hardie, J. A. Hutchings, D. E. Ruzzante, C. T. Taggart, and P. Bentzen.
2010. Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. R. Proc. Soc. B. doi:277(1701)3725–3734. 10.1098/rspb.2010.0985.

Chambers, R. C., Leggett, W. C., and J. A. Brown.
1989. Egg size, maternal effects and the correlations between early life history traits of capelin, *Mallotus villosus*: an appraisal at the individual level. Fish. Bull. 87:515–523.

Geffen, A. J.
2002. Length of herring in relation to age and time of hatching. J. Fish Biol. 60:479–485.

Houde, E. D.
2008. Emerging from Hjort's shadow. J. Northw. Atl. Fish. Sci. 41:53–70.

Hunt, G. L., Jr, P. Stabeno, G. Walters, E. Sinclair, R. D. Brodeur, J. M. Napp, and N. A. Bond.
2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res., pt. II, 49:5821–5853.

Hurst, T. P., and A. A. Abookire.
2006. Temporal and spatial variation in potential and realized growth rates of age-0 northern rock sole. J. Fish Biol. 68:905–919.

Hurst, T. P., A. A. Abookire, and B. Knoth.
2010. Quantifying thermal effects on contemporary growth variability to predict responses to climate change in northern rock sole (*Lepidopsetta polyxystra*). Can. J. Fish. Aquat. Sci. 67:97–107.

Hurst, T. P., and T. A. Duffy.
2005. Activity patterns in northern rock sole are mediated by temperature and feeding history. J. Exp. Mar. Biol. Ecol. 325:201–213

Ims, R. A.
1990. The ecology and evolution of reproductive synchrony. Trend. Ecol. Evol. 5:135–140.

Jobling, M.
1997. Temperature and growth: modulation of growth rate via temperature change. *In* Global warming: implications for freshwater and marine fish (C. M. Wood and D. G. McDonald, eds.), p. 223–254. Cambridge Univ. Press, Cambridge, U.K.

Jordaan, A., and L. J. Kling.
2003. Determining the optimal temperature range for Atlantic cod (*Gadus morhua*) during early life. *In* The big fish bang (H. I. Browman and A. B. Skiftesvik, eds.), p. 45–62. Inst. Mar. Res., Bergen, Norway.

Lanksbury, J. A., J. T. Duffy-Anderson, K. L. Mier, M. S. Busby, and P. J. Stabeno.
2007. Distribution and transport patterns of northern rock sole, *Lepidopsetta polyxystra*, larvae in the southeastern Bering Sea. Prog. Oceanogr. 72:39–62.

Laurel, B. J., and I. R. Bradbury.
2006. "Big" concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. Can. J. Fish. Aquat. Sci. 63:2603–2607.

Laurel, B.J., L. A. Copeman, T. P. Hurst, and M. W. Davis.
2008. The role of temperature on the growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*). J. Plank. Res. 30:1051–1060.

Laurel, B. J., A. W. Stoner, and T. P. Hurst.
2007. Density-dependent habitat selection in marine flatfish: the dynamic role of ontogeny and temperature. Mar. Ecol. Prog. Ser. 338:183–192.

Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of Northeast Pacific fishes. NOAA Tech. Rep. NMFS 80, 652 p.

Matarese, A. C., D. M. Blood, S. J. Picquelle, and J. L. Benson.
2003. Atlas of abundance and distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972–1996). NOAA Prof. Pap. NMFS 1, 281 p.

Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson.
2002. Fishes of Alaska, 1037 p. Am. Fish. Soc., Bethesda, MD.

Methven, D. A., and J. A. Brown.
1991. Time of hatching affects development, size, yolk volume, and mortality of newly hatched *Macrozoarces*

americanus (Pisces: Zoarcidae). Can. J. Zool. 69:2161–2167.

O'Connor, M. I., J. F. Bruno, S. D. Gaines, B. S. Halpern, S. E. Lester, B. P. Kinlan, and J. M. Weiss.
2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Natl. Acad. Sci. 104:266–1271.

Orr, J. W., and A. C. Matarese.
2000. Revision of the genus *Lepidopsetta* Gill, 1862 (Teleostei: Pleuronectidae) based on larval and adult morphology, with a description of a new species from the North Pacific Ocean and Bering Sea. Fish. Bull. 98:539–582.

Panagiotaki, P., and A. J. Geffen.
1992. Parental effects on size variation in fish larvae. J. Fish Biol. 41:37–42.

Paulsen, H., O. S. Kjesbu, V. Buehler, R. A. J. Case, C. Clemmesen, G. Carvlho, L. Hauser, W. F. Hutchinson, E. Moksness, H. Ottera, A. Thorsen, and T. Svasand.
2009. Effects of egg size, parental origin and feeding condition on growth of larval and juvenile cod *Gadus morhua*. J. Fish. Biol. 75:516–537.

Pauly, D. and R. S. V. Pullin.
1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes 22:261–271.

Pena, M., A. Uriarte, M. Santos, and L. Ibaibarriaga.
2010. A maximum likelihood method for obtaining incubation temperature of eggs of synchronous spawning fishes. Fish. Res. 103:9–17.

Pepin, P.
1991. The effect of temperature and size on development and mortality rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Pertseva-Ostroumova, T. A.
1961. The reproduction and development of far eastern flounders. Tr. Inst. Okeanol. Akad. Nauk SSR. [In Russian; English transl., Fish. Res. Board Can., Transl. Serv. 856, p. 493–519, 1967.]

Porter, S. M., and K. M. Bailey.
2007. The effect of early and late hatching on the escape response of walleye pollock (*Theragra chalcogramma*) larvae. J. Plankton Res. 29:291–300.

Ringo, E., R. E. Olsen, and B. Boe.
1987. Initial feeding of wolffish (*Anarhichas lupus*) fry. Aquaculture 62:33–43.

Stark, J. W., and D. A. Somerton.
2002. Maturation, spawning and growth of rock soles off Kodiak Island in the Gulf of Alaska. J. Fish Biol. 61:417–431.

Comparison of life history parameters for landed and discarded fish captured off the southeastern United States

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Abstract—Commercial fisheries that are managed with minimum size limits protect small fish of all ages and may affect size-selective mortality by the differential removal of fast growing fish. This differential removal may decrease the average size at age, maturation, or sexual transition of the exploited population. When fishery-independent data are not available, a comparison of life history parameters of landed with those of discarded fish (by regulation) will indicate if differential mortality is occurring with the capture of young but large fish (fast growing phenotypes). Indications of this differential size-selective mortality would include the following: the discarded portion of the target fish would have similar age ranges but smaller sizes at age, maturation, and sexual transition as that of landed fish. We examined three species with minimum size limits but different exploitation histories. The known heavily exploited species (*Rhomboplites aurorubens* [vermilion snapper] and *Pagrus pagrus* [red porgy]) show signs of this differential mortality. Their landed catch includes many young, large fish, whereas discarded fish had a similar age range and mean ages but smaller sizes at age than the landed fish. The unknown exploited species, *Mycteroperca phenax* (scamp), showed no signs of differential mortality due to size-selective fishing. Landed catch consisted of old, large fish and discarded scamp had little overlap in age ranges, had significantly different mean ages, and only small differences in size at age when compared to comparable data for landed fish.

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Size limits are commonly used to manage commercial and recreational fisheries. Minimum size limits, which are relatively easy to enforce, have been used to restrict total harvest, prevent growth overfishing (where fish are harvested at an average size smaller than the size needed to produce maximum yield per recruit), and allow individuals at least one spawning event before removal from the fishery (Pitcher and Hart, 1982; Rothschild, 1986). One widely acknowledged disadvantage of size limits is the mortality immediately at release (release mortality) for under-size fish, but another emerging concern is that size-selective fisheries drive a phenotypic change in the life history traits of a population (Stokes and Law, 2000; Hutchings, 2005; Williams and Shertzer, 2005; Swain et al., 2007). Observed phenotypic changes can be driven by genetic and environmental influences. If the observed phenotypic change is mostly influenced by environmental changes (e.g., fishing pressure), then the observed phenotype may easily be reversed by adjusting the environmental influence, whereas if the change is largely influenced by genetic changes, it may not be readily reversed.[1] Recent studies have shown that high levels of fishing pressure can create changes in size at age, age at maturation, and size at maturation (Law, 2000; Heino and Godø, 2002; Grift et al., 2003; Olsen et al., 2005; Kuparinen and Merilä, 2007; Mollet et al., 2007; Sharpe and Hendry, 2009). In long-lived species, the decrease in individual growth rates, caused by early maturation in response to size-selective mortality, may have a severe effect on the stock. High levels of fishing pressure can not only decrease size at maturation, which results in an overall decrease in size at age, but because fecundity is correlated with size (Buckley et al., 1991; Hutchings and Meyers, 1993; Kjesbu et al., 1996; Trippel et al., 1997), high fishing pressure can also decrease reproductive potential of a population (Ratner and Lande, 2001). That these phenotypic shifts not only occur, but occur within several generations has been documented in several experimental studies (Reznick et al., 1990; Conover and Munch, 2002; Conover et al., 2005; Reznick and Ghalambor, 2005; Walsh et al., 2006).

Size limits are intended to protect fished populations by allowing young, small fish to grow larger and spawn at least once before capture, and thereby increase long-term yield (Ricker, 1945; Goodyear, 1996; Coleman et al., 2000). However, minimum size limits can increase fishing mor-

[1] Law, R. 2002. Selective fishing and phenotypic evolution: past, present, and future. ICES CM 2002/Y:11, 9 p.

tality on faster-growing phenotypes that reach the minimum size limit at a young age. Size limits protect all small fish of all ages, and over time small fish of all ages may dominate the population, because they have more opportunities to reproduce before removal from the population. Size at age and size at maturation may decrease in response to a higher proportion of slower growing phenotypes in the population (Pitcher and Hart, 1982). Such changes may result in decreased population abundance and biomass (Kuparinen and Merilä, 2007).

All current indications of phenotypic shifts for reef species off the coast of the southeastern United States have been derived solely from fishery-independent research surveys (Harris and McGovern, 1997; Zhao et al., 1997; Harris et al., 2002). Yet for many reef species in this region, there is not enough fishery-independent data to make this determination. When a lack of such data occurs, there are only fishery-dependent data sources available to determine if phenotypic shifts are occurring. To the authors' knowledge no one has used fishery-dependent data from commercial or recreational harvests to confirm whether or not the selective harvest of fast growing phenotypes is creating a phenotypic shift in fished populations. By comparing the life history parameters of landed (legal size) fish to those of regulatory (sublegal size) discards, one can determine if the minimum size limit is an appropriate management technique for a given species. If a phenotypic shift towards small, slow growing fish is occurring, then the discarded portion of the catch when compared to the landed portion should show similar age ranges, smaller size at age, smaller size at maturity, and smaller size at sexual transition for hermaphroditic species. Alternatively, if no phenotypic shift is occurring, then the discarded portion of the catch would consist almost exclusively of young, immature fish (although maturity stage would vary depending on the minimum size limit and species being investigated).

The South Atlantic Fisheries Management Council (SAFMC) is responsible for managing stocks in federal waters from North Carolina to Key West, Florida. Size limits (supplemented by seasonal closures for some species) have been the preferred regulatory control measure of the SAFMC since the development of the Fishery Management Plan for the snapper grouper fishery of the South Atlantic Region in 1983 (SAFMC, 1983). We investigated whether minimum size limits are contributing to a phenotypic shift towards small, slow growing phenotypes for three managed species of the snapper-grouper complex at different levels of exploitation: vermilion snapper (*Rhomboplites aurorubens*), currently experiencing overfishing with a fishing mortality rate (F) of 0.49 (SEDAR, 2008); red porgy (*Pagrus pagrus*), currently considered overfished, with predicted F of 0.095 (SEDAR, 2006); and scamp (*Mycteroperca phenax*), last classified as experiencing overfishing in 1998 (Manooch et al., 1998).

Table 1

The total number of days when samples of fish were collected by commercial fishermen off the coast of southeastern United States for each month within each year.

Month	2005	2006	2007	Total
January		10	5	15
February		10	10	20
March		12	8	20
April		7	8	15
May		16	14	30
June		3	8	11
July	10	8	6	24
August	9	13	4	26
September	13	14	7	34
October	11	13		24
November	6	11		17
December	8	2		10

Materials and methods

Sampling took place on a South Carolina commercial snapper-grouper fishing vessel from July 2005 through September 2007 and consisted of 52 trips (246 sampled days) across all months (Table 1). The vessel captain dedicated the last few days of each trip (trips ranged between five and nine days) to collecting samples, when he would retain all legal and sublegal size fish of vermilion snapper, red porgy, and scamp. The sampling locations were selected by the captain as part of his normal fishing routine. Fishing locations were situated from 30°16.558′N to 33°36.795′N, and most locations were along the shelf-break (Fig. 1). Sampling depths ranged between 20 and 128 m. Three bandit-reels, with terminal tackle consisting of two 4/0 J-hooks and baited with mackerel (*Sarda sarda*), were fished simultaneously by three crew members, and all fishing took place from sunrise to sunset. For each location, the captain recorded the position (latitude and longitude) and depth. Fish were tagged with a numbered t-bar tag (Floy Tag, Inc., Seattle, WA) and immediately placed on ice to preserve reproductive tissue in samples. Up to 90 sublegal and legal size fish of each species were kept from each trip, for up to 500 fish per species for each of two size categories (legal and sublegal) per year of the study. All fish were immediately collected from the captain upon returning to port and transported to the laboratory.

In the laboratory individual weight (g) and lengths (total [TL], fork [FL], and standard length [SL]; mm) were measured for each fish sampled. Both sagittal otoliths were removed and stored dry in coin envelopes. A posterior section of each gonad was removed and stored in 10% buffered seawater formalin. Although the sampling period was limited to one experienced commercial fisherman's catch over multiple

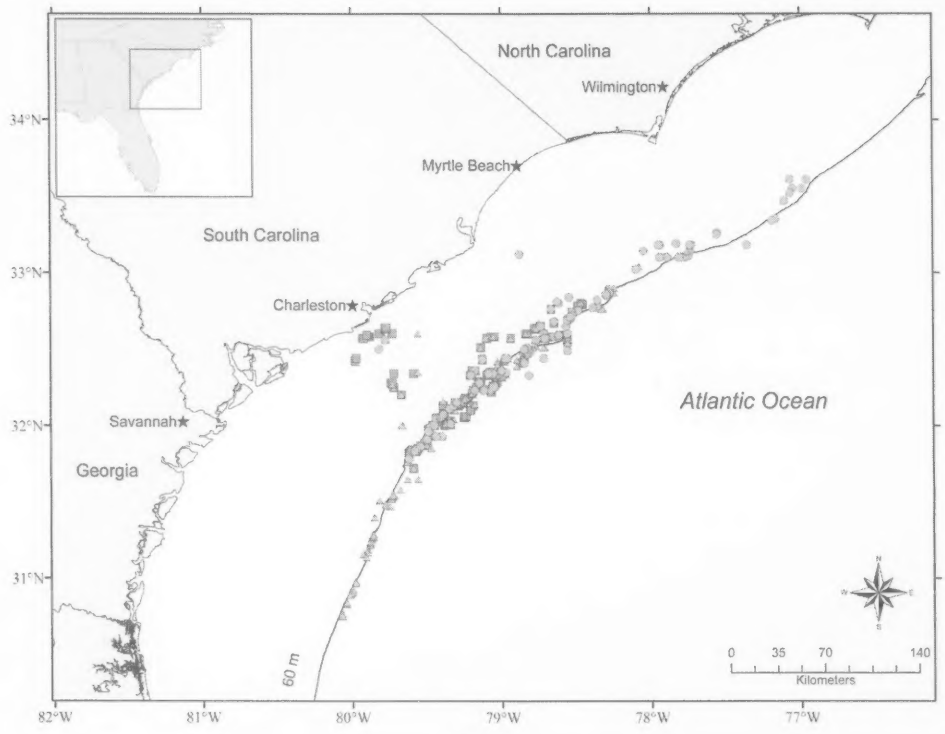

Figure 1

Fishing locations selected by the commercial fishermen for collections of vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*). General sampling locations overlapped among years (square=2005; triangle=2006; circle=2007) and were primarily on the shelf-break.

years, his catches were typical of catches for commercial snapper-grouper fishermen in this region (Stephen and Harris, 2010).

Age and growth

Vermilion snapper and scamp otoliths were embedded in epoxy resin, sectioned through the core (~0.7 mm) with a Buehler IsoMet low-speed saw (Buehler, Lake Bluff, IL), and mounted on glass slides. All red porgy otoliths were first read whole. Otoliths from fish older then 6+ years were also sectioned and read to ensure accurate determination of age. Increments, defined as one translucent and one opaque zone for all species, were counted independently by two readers. Readers had no prior knowledge of the length, weight, sex, or capture date for any fish. Readers counted increments on sectioned otoliths along the dorsal side of the sulcus acousticus, from the core to the outer edge of the otolith and qualitatively ranked the edge type and otolith quality. For whole otoliths, increments were counted along a straight line midway between the posterodorsal dome and the most posterior point on the otolith. Edge types were categorized as either 1) an opaque zone on the otolith edge; 2) a narrow translucent zone on the otolith edge; 3) a medium translucent zone on the otolith edge; or 4) a wide translucent zone on the otolith edge. Edge type and increment count were used to assign an age to each fish. For otoliths with a medium or wide translucent zone (edge type 3 or 4) in fish captured after January 1 but before the month of opaque zone formation (vermilion snapper=September [Zhao et al., 1997]; red porgy=June [Harris and McGovern, 1997]; scamp=April [Harris et al., 2002]), ages equaled the increment count plus one; for all other fish, the age equaled the increment count.

For vermilion snapper and scamp otoliths, two readers independently counted the increments for all fish. Total agreement, agreement within one increment, and average percent error (APE) were calculated for both vermilion snapper and scamp readings. For both species, readers simultaneously re-examined otoliths when increment count or edge type did not agree. If readers could not agree on a count and edge type, that otolith was not used in analyses. For red porgy otoliths, the first reader aged all otoliths, and a second reader aged a subset (n=100 otoliths). Because there was a 98% agreement within one year, all final readings were from the first reader.

Age distributions for sublegal and legal size fish were compared by using a Kolmogorov-Smirnov two sample

test. Sublegal and legal mean ages were compared using a one-way ANOVA. Proportions of sublegal and legal fish within each age class were compared by using a 2x2 contingency table with a chi-square test statistic or Fisher's test statistic when cell sizes were low. Mean lengths of sublegal and legal size fish within each age class where compared by using individual one-way ANOVAs. For comparison with other studies, total lengths were converted to fork lengths based on equations generated from the 30+ year collaborative fishery-independent reef fish survey program MARMAP (Marine Resources Monitoring, Assessment, and Prediction) (M. Reichert, unpubl. data) (Table 2). All statistical analyses were done in SAS, vers. 9.2 (SAS Institute Inc., Cary, NC).

Reproduction

Reproductive tissues were stored in 10% buffered seawater formalin for 1–2 weeks, after which samples were transferred to 50% isopropanol for 1–2 weeks. Reproductive tissues were then vacuum-infiltrated in a tissue processor, blocked in paraffin, and sectioned (7 µm) on a rotary microtome. Three sections from each sample were placed on a glass slide, stained with double-strength Gill's hematoxylin, and counter-stained with eosin-Y (Schmidt et al., 1993). Each section was viewed under a compound microscope (40–400× magnification) to determine sex and reproductive state by criteria modified from Harris et al. (2001). Correct assignment of reproductive stage was confirmed through length histograms by reproductive state (immature and mature), in which there was little overlap in the tails of the distribution (Wyanski et al., 2000).

Sex ratios (male:female) were compared to 1:1 ratios by using the chi-square goodness-of-fit test. The chi-square test (large sample sizes) or Fisher's exact test (small sample sizes) were used to compare sex ratios of legal and sublegal size fish. Probability of maturation and transitions at length and age were calculated with the maximum likelihood estimates, and the Wald's chi-square test statistic was used to compare probability estimates between sublegal- and legal-size fish.

Results

Vermilion snapper

A total of 1739 vermilion snapper were collected, of which 845 were legal-size (>305 mm TL) and 894 sublegal-size fish. Of these, 1638 were successfully aged. Age ranges were similar between legal- (1–10 years) and sublegal-size (0–12 years) vermilion snapper, but the distributions were significantly different (Kolmogorov-Smirnov test statistic [D]=0.29, P<0.001) (Fig. 2A). As expected, the younger age classes (0–3 years) were predominantly sublegal size fish, whereas the older ages were predominately legal size. Mean age (3.5 yr) of sublegal-size fish was significantly different from the mean age (4.5 yr; F=196, P< 0.001, degrees of freedom [df]=1) of legal-size fish. Proportions within each age class were significantly different except for age four (χ^2=2.779, P=0.096, d.f.=1), where sublegal-size fish represented 46% of the catch (Fig. 2A). Sublegal vermilion snapper consistently had significantly smaller sizes at age for all comparable (n>3 per classification) age classes (F values between 7.0 and 509.7, P values between 0.0181 and <0.001, df=1; Fig. 3A).

Table 2

The linear relationship (with coefficient of determination [r^2]) between total length (TL) and fork length (FL) for vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) based on lengths collected through the 30+ year fishery-independent reef fish MARMAP (Marine Resources Monitoring, Assessment and Prediction) survey off the coast of the southeastern United States. n=number of fish in samples for each species.

Species	FL–TL relationship	n	r^2
Vermilion snapper	FL=0.8948TL+1.127	13,249	0.9964
Red porgy	FL=0.8700TL+0.290	16,498	0.9924
Scamp	FL=0.8745TL+26.903	2910	0.9883

Sex and maturity status were assigned to 1708 vermilion snapper. Vermilion snapper sex ratios (M:F) of sublegal-size fish favored males (1:0.81; χ^2=9.2, P=0.002, df=1), whereas there was no difference from a 1:1 ratio for legal-size vermilion snapper (1:0.92; χ^2=1.4, P=0.237, df=1). Sex ratios were not statistically different between legal- and sublegal-size vermilion snappers (χ^2=3.2, P=0.07, df=1). Sex ratios for legal and sublegal sizes were not statistically different within age classes, except for age three (legal-size fish=1:1.10, sublegal-size fish=1:0.55; χ^2=8.9, P=0.002, df=1).

Size at 50% maturity could not be determined for legal-size vermilion snapper because all legal-size fish were mature. In fact, all males in this study were mature, across all lengths (111–470 mm FL) and ages (0–12 years). There were 31 (3.9%) immature female sublegal vermilion snapper in our sample ranging in age from 0 to 2 years (Table 3) and in size from 99 mm to 257 mm FL (Table 4). Including all females, of legal and sublegal size, length at 50% maturity was estimated at 212 mm FL (95% confidence intervals [CI]=197–220 mm FL) and 100% maturity was reached by 258 mm FL.

Red porgy

A total of 2009 red porgy were collected, of which 1014 were legal size (>356 mm TL) and 1005 were sublegal-size fish. Of these, 2010 fish were successfully aged. Age ranges were similar between legal-size (0–14 years) and sublegal-size (0–12 years) red porgy, but the distribu-

tions were significantly different (D=0.37, P<0.001), with mean ages differing by one year (Fig. 2B). Red porgy aged seven and older represented a small portion of the catch for both legal- and sublegal-size fish, and the average age of legal-size fish was 4.5 years (±1.61 standard deviation [SD)]). Mean age at sublegal size was significantly different from mean age (F=369.68, P<0.001, df=1) at legal size and proportions within each age class were significantly different (χ^2 values between 7.35 and 123.60, P values between 0.006 and <0.001, df=1). Sublegal-size red porgy consistently had significantly smaller sizes at age for all comparable (n>3 per classification) age classes (F values between 11.85 and 1078.56, P values between 0.002 and <0.001, df=1; Fig. 3B).

Sex and maturity status were assigned to 1894 red porgy (955 males and 939 females). Sex ratios were significantly different from 1:1 (legal-size fish χ^2=15.6, P<0.001, df=1 and sublegal-size fish χ^2=29.6, P<0.001, df=1). As expected for a protogynous species, sex ratios for sublegal-size red porgy favored females (1:1.43) and for legal-size red porgy, ratios favored males (1:0.77). Sex ratios by age classes were not significantly different, except for age five (legal-size fish 1:0.64 and sublegal-size fish 1:1.24; χ^2=7.80, P=0.005, df=1). Because of the limited number of immature females (n=23; 1.1%), size at maturity estimates could not be determined. The two immature legal-size red porgy were both four years old, and the remaining immature sublegal red porgy (n=21) were between one and five years old (Table 3). Immature female lengths ranged between 150 and 346 mm FL (Table 4). Sexually transitioning red porgy (n=266) were between zero and eight years old, of which 144 were sublegal-size and 122 were legal-size fish. Eleven of the transitional fish were juveniles, that is immature females that have transitioned to male (primary male), and all were sublegal size. Age at 50% sexual transition was not significantly different (Wald's χ^2=1.02, P=0.312, df=1) between legal- and sublegal-size red porgy and occurred around age two (legal-size fish=2.17 yr and sublegal-size fish=2.23 yr). All red porgy were male by age 10. There were not enough data to conduct an analysis of length at sexual transition. Sexually transitioning red porgy were between 215 and 416 mm FL and 47% of the transitioning red porgy were at or over the legal minimum size limit.

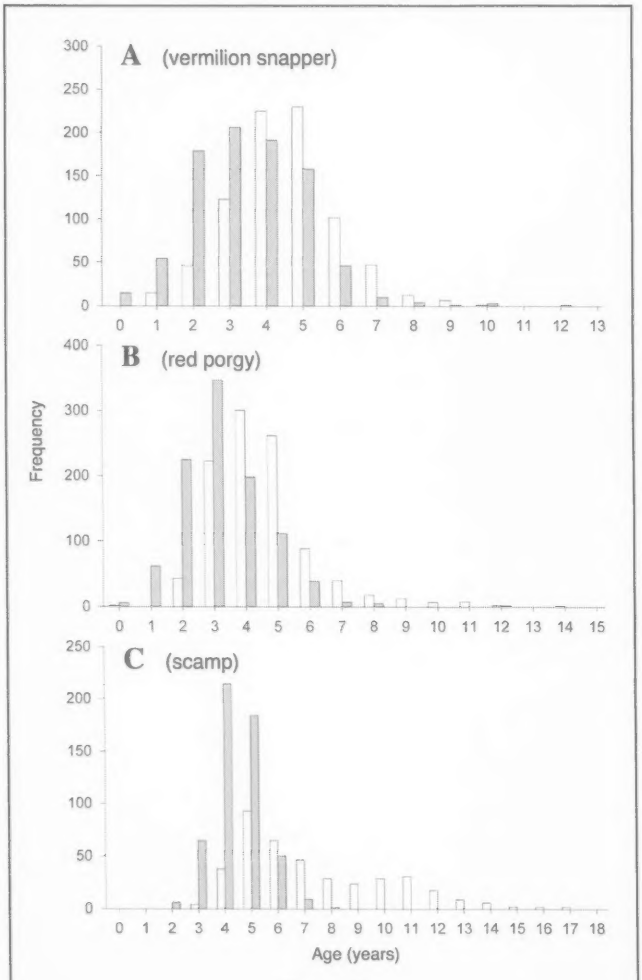

Figure 2

Age-frequency distributions for sublegal- (gray) and legal-size (white) fish by species: (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp). Fish were collected by commercial fishermen off the coast of the southeastern United States from 2005 through 2007.

Scamp

A total of 952 scamp were collected, of which 409 were legal-size (>508 mm TL) and 543 were sublegal-size fish. Of these, 927 were successfully aged. There was a narrow range of overlapping age ranges for sublegal-size (2–8 years) and legal-size (3–17 years) scamp (Fig. 2C), and the distributions were significantly different (D=0.11, P=0.006). The sublegal-size scamp distribution was narrow and peaked at ages four and five, whereas the legal size distribution was platykurtic (kurtosis=0.09) and left skewed. Mean age for sublegal-size fish was significantly different from mean age at legal sizes(F=485.1, P<0.001, df=1) and proportions of legal- and sublegal-size scamp within each age class were significantly different, except for age 6 (χ^2=1.95, P=0.162, df=1). Legal-size scamp were significantly larger at age than sublegal-size scamp

for all ages (F values from 26.8 to 497.4, all P values were <0.001, df=1; Fig. 3C).

Sex and maturity status were assigned to 943 scamp (821 females and 122 males). Sex ratios of legal- and sublegal-size fish were significantly different from 1:1 (legal-size fish: χ^2=68.5, P<0.001, df=1; sublegal-size fish: χ^2=525.1, P<0.001, df=1). There were low numbers of males captured, and sex ratios favord females for both legal- and sublegal-size scamp (legal-size fish 1:2.40 and sublegal-size fish 1:134.25). Immature scamp were between two and six years old (Table 3) and 307 to 473 mm FL (Table 4). Because a limited number of immature legal females were collected (n=2), probability of maturity at size and age were calculated by using both legal- and sublegal-size fish. Length and age at 50% maturity were estimated at 331 mm FL and two years, and length and age at 100% maturation were estimated at 474 mm FL and seven years, respectively. Sexual transition occurred over a wide range of ages and lengths (3–13 years; 440–720 mm FL; n=26) and consisted entirely of adult fish. Probabilities of sexual transition were calculated from the entire data set because of the low number of sublegal-size males. Length at 50% and 100% sexual transition were 629 mm FL and 740 mm FL, respectively, whereas age at 50% sexual transition was 9.7 years and at 100% sexual transition, 14 years.

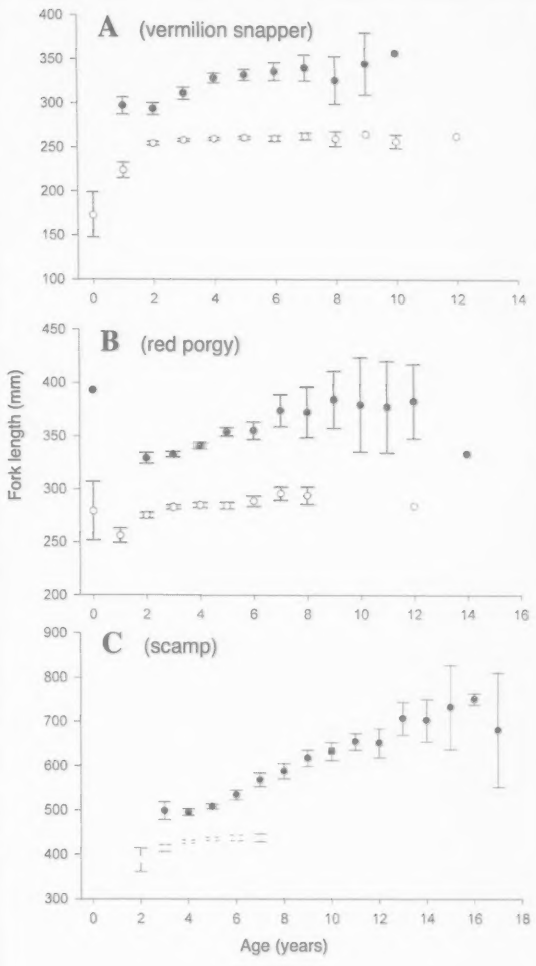

Figure 3

Mean fork length at age (±2 standard errors) for sublegal- (white) and legal-size (black) fish by species: (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp).

Discussion

Vermilion snapper

Vermilion snapper were reported in the South East Data, Assessment, and Review (SEDAR) 2008 stock assessment as experiencing overfishing, but were not overfished, with an F of 0.49 (SEDAR, 2008). This species has been managed with a 12 inch TL (274 mm FL) commercial minimum size limit since 1999. Despite the minimum size limit regulation, F has continued to increase (SEDAR, 2008). The comparison of the life history parameters of commercially caught legal- and sublegal-size vermilion snapper show that commercial fishing crews are capturing young, but large vermilion snapper—a fast growing phenotype. Comparing growth curves to previous time periods (1979–81 and 1985–93, Zhao et al., 1997), we found an increased growth rate for the current time period, particulary for the young fish (<5 yr), although asymptotic length, L_∞, values are similar to those found from 1979 to 1981 (Fig. 4A). This increased growth rate allows fish to reach the minimum size limit at an earlier age. Interestingly, the L_∞ for this study is only 25 mm greater than the minimum size limit.

Size at maturity is not a good indicator of differential fishing pressure on fast growing phenotypes for vermilion snapper because all immature fish in the collections were female and sublegal. This is not an unexpected result because vermilion snapper mature at a very small size and age. In a study on the reproductive biology of vermilion snapper, Cuellar et al. (1996) found no immature fish (n=1004, size range=165–375 mm FL). Comparison with other studies (Zhao and McGovern, 1997), shows that vermilion size and age at maturity has decreased since the 1980s, a period when maximum length decreased.

The observed sex ratios in our study favored males, in contrast to either 1:1 ratios or more females from other studies (Zhao and McGovern, 1997; Hood and Johnson, 1999; Allman, 2007; SEDAR, 2008). These differences may be attributed to location and gear selectivity. Hood and Johnson (1999) noted that the ver-

Table 3

Percentage of mature fish by age class for female vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) by sublegal- and legal-size classification. All fish were examined histologically. (*n*)=number of fish in samples.

	Vermilion snapper		Red porgy		Scamp	
Age (yr)	Sublegal size % (*n*)	Legal size % (*n*)	Sublegal size % (*n*)	Legal size % (*n*)	Sublegal size % (*n*)	Legal size % (*n*)
0	22 (9)	—	100 (1)	100 (1)	—	—
1	52 (31)	100 (9)	67 (33)	—	—	—
2	94 (94)	100 (22)	97 (119)	100 (28)	33 (3)	—
3	100 (71)	100 (64)	99 (161)	100 (107)	77 (44)	50 (2)
4	100 (74)	100 (106)	98 (91)	99 (137)	93 (178)	100 (30)
5	100 (81)	100 (109)	94 (53)	100 (98)	97 (156)	100 (73)
6	100 (17)	100 (47)	100 (15)	100 (31)	100 (44)	98 (49)
7	100 (2)	100 (13)	100 (2)	100 (10)	100 (8)	100 (36)
8	100 (2)	100 (2)	100 (2)	100 (4)	100 (1)	100 (20)
9	—	100 (4)	—	100 (2)	—	100 (11)
10	—	100 (1)	—	—	—	100 (13)
11	—	—	—	—	—	100 (13)
12	—	—	—	—	—	100 (5)

milion sex ratio (generally 1:1) in the Gulf of Mexico was different from sex ratios found off the coast of the southeastern United States. Zhao and McGovern (1997) noted that traps caught more females than hook-and-line or trawl gear. All of our catches were from hook-and-line gear that was fished about 3 m off the bottom, rather than from on-bottom gear (e.g., traps). If vermilion snapper schools segregate by sex, with males higher in the water column, it is possible that the males would encounter the baited hooks first. The difference in sex ratios is of utmost concern because it will have significant impact in fishery stock assessment models. Such a study as that performed by DeVries (2006), who looked at size- and sex-induced fish behavior bias, is needed to determine the cause of this difference and which sex ratio is more indicative of the population.

Red porgy

The 2006 SEDAR stock assessment of red porgy, a protogynous hermaphrodite, concluded that although this stock was not experiencing overfishing, it was overfished (SEDAR, 2006). A commercial 12 inch TL (307 mm FL) minimum size limit for red porgy was introduced in 1992, but fishing mortality remained high from 1992 through 1998, with F values between 0.44 and 0.75 (SEDAR, 2006). In 1999, the minimum size limit was increased to a 14 inch TL (307 mm FL), a seasonal closure (from May to December) was instituted, as well as an emergency closure from September 1999 through August 2000. In late 2000, a commercial trip limit on catch (50 lb/trip) was established, and in 2006 this was modified to 120 fish/trip or a 127,000 lb gutted yearly quota. Since 2001, F has continued to decrease (F=0.078 in 2004) and spawning stock biomass has increased (SEDAR, 2006).

Commercial fishermen are harvesting faster growing (young but large) fish. In our study the sublegal- and legal-size portions of the population had broad overlapping age ranges, and mean ages differed by only one year. The age-frequency distributions for legal red porgy were left-skewed (skewness=1.5) and had a high peak (kurtosis=4.13) that indicated high fishing mortality occurring on ages four and five. Red porgy are a relatively long-lived species with a maximum age of 18 years (Potts and Manooch, 2002), and yet red porgy 10 years and older were <1% of the catch. Interestingly, the majority of all red porgy being captured are between ages three and five, indicating that there is a lack of not just large fish, but also old fish in the population. For a species known to live 18 years, these values indicate a considerable change in the population structure because many of the older fish have been removed. Comparison of von Bertalanffy curves (Fig. 4B) with those of previous studies (Manooch and Huntsman, 1977; Harris and McGovern, 1997) show that current growth rates are greater than those in earlier time periods (1979–81 and 1988–90). Interestingly, the asymptotic length is only 20 mm higher than the minimum size limit. Maturity in red porgy in our study occurred as early as less than one year in both legal- and sublegal-size specimens, and by age one, over 60% of the sublegal-size specimens were considered mature, indicating that maturation is occurring at a young age and small size. This is consistent with the findings from Harris and McGovern (1997) and Hood and Johnson (2000) who also noted mature females at a small sizes and ages. Our age of 100% female maturation, age six, was two years older than that reported in the Hood and Johnson (2000)

Table 4

Percentage of mature fish by length interval for female vermilion snapper (*Rhomboplites aurorubens*), red porgy (*Pagrus pagrus*), and scamp (*Mycteroperca phenax*) by sublegal and legal classification. All fish were examined histologically. *n*=number of fish in samples.

	Vermilion snapper			Red porgy			Scamp		
Fork length (mm)	Age range	Sublegal size % (*n*)	Legal size % (*n*)	Age range	Sublegal size % (*n*)	Legal size % (*n*)	Age range	Sublegal size % (*n*)	Legal size % (*n*)
101–120	0–1	0 (3)	—	—	—	—	—	—	—
121–140	0	0 (1)	—	—	—	—	—	—	—
141–160	0	0 (3)	—	1	0 (1)	—	—	—	—
161–180	0–1	0 (3)	—	—	—	—	—	—	—
181–200	0–1	100 (1)	—	1–2	0 (2)	—	—	—	—
201–220	0–2	47 (15)	—	0–1	100 (3)	—	—	—	—
221–240	1–6	81 (43)	—	1–4	63 (11)	—	—	—	—
241–260	0–10	97 (153)	—	1–6	89 (55)	—	—	—	—
261–280	0–12	100 (171)	100 (48)	0–8	97 (147)	—	—	—	—
281–300	1–9	—	100 (69)	0–12	98 (193)	—	—	—	—
301–320	1–9	—	100 (68)	0–11	100 (67)	100 (102)	—	0 (1)	—
321–340	1–9	—	100 (63)	2–14	—	99 (131)	2–4	0 (1)	—
341–360	2–10	—	100 (45)	2–11	—	99 (103)	3–5	67 (6)	—
361–380	3–8	—	100 (35)	2–12	—	100 (45)	2–5	83 (18)	—
381–400	3–7	—	100 (25)	0–12	—	100 (15)	2–6	88 (26)	—
401–420	3–9	—	100 (23)	4–11	—	100 (9)	2–7	85 (59)	—
421–440	3–8	—	100 (7)	5–9	—	100 (7)	2–8	97 (135)	—
441–460	4–7	—	100 (7)	5–9	—	100 (4)	3–7	97 (143)	—
461–480	5–7	—	100 (7)	5–8	—	100 (5)	3–6	96 (54)	94 (31)
481–500	—	—	—	11	—	100 (1)	3–17	—	100 (46)
501–520	—	—	—	—	—	—	3–8	—	100 (40)
521–540	—	—	—	—	—	—	3–12	—	100 (31)
541–560	—	—	—	—	—	—	4–12	—	100 (25)
561–580	—	—	—	—	—	—	5–11	—	100 (21)
581–600	—	—	—	—	—	—	5–14	—	100 (22)
601–620	—	—	—	—	—	—	5–17	—	100 (9)
621–640	—	—	—	—	—	—	7–13	—	100 (11)
641–660	—	—	—	—	—	—	6–13	—	100 (10)
661–680	—	—	—	—	—	—	7–11	—	100 (8)
681–700	—	—	—	—	—	—	7–15	—	100 (2)
701–720	—	—	—	—	—	—	10–12	—	100 (2)
721–740	—	—	—	—	—	—	10–14	—	100 (2)

study, showing a shift to older age at maturation. This may be a response to the reduced fishing mortality that was instituted to rebuild the stock.

Age at transition was similar for both sublegal- and legal-size red porgy, indicating that different growth rates did not affect the age of sexual transition. Instead, sexual transition may be related to other factors, particularly local social dynamics. In fact, size at transition does not appear to have changed much over time. Although age at transition in our study (two years) was younger than previously reported values of 3.5–5 years (Hood and Johnson, 2000; Daniels, 2003), mean size of transitional fish was similar (Daniels, 2003; Harris, 2003). Using Allsop and West's (2003) formulas to estimate age (2.5×age at maturity) and size at transition (80% of maximum body size), we found that the expected age at transition was similar to the observed value and the expected size at transition was within the range of the observed transitioning fish. Sex ratios at age in our study support these estimates, because by age 2 sex ratios are approximately 1:1.15, by ages 3 and 4 are close to 1:1, and by age 5 favor males. Similarly, sex ratios for red porgy smaller than 320 mm FL favored females, between 320 and 359 mm FL were close to 1:1, and favored males after 360 mm FL. Primary males (juvenile transitional fish) are often a socially mediated plastic response to high population densities or sex ratios that severely favor females (Liu

and Sadovy, 2004; Munday et al., 2006a; Munday et al., 2006b). The low number of juvenile transitional fish is indicative of a stable sex ratio in the red porgy population, low to moderate local red porgy densities, or any combination thereof.

There are a variety of fishing regulations for red porgy that may act to counter differential fishing mortality on young, large fish. Red porgy currently have a commercial minimum size limit, a 120 fish/trip limit, seasonal closure, and a total gutted weight quota [SAFMC[2]]. Despite these regulations, red porgy continue to be hooked throughout the year or after a limit has been reached because of their close association with other targeted snapper-grouper species. These red porgy must be discarded, but, as a study from Stephen and Harris (2010) indicated, all sizes may experience high immediate release mortality. During the closed season or after trip limits or quotas are reached, all red porgy experience the same release mortality, and this mortality counteracts any differential fishing mortality. Furthermore, discarded sublegal-size red porgy are also experiencing a high release mortality that may remove many of the small old fish from the population.

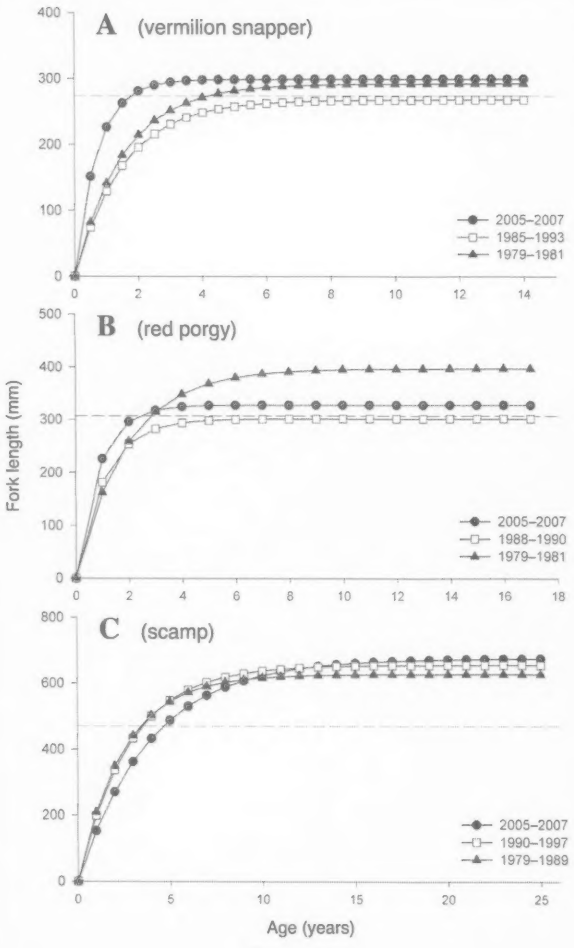

Figure 4

Comparison of von Bertalanffy growth curves from various locations in the Atlantic Ocean for (**A**) *Rhomboplites aurorubens* (vermilion snapper), (**B**) *Pagrus pagrus* (red porgy), and (**C**) *Mycteroperca phenax* (scamp). All curves represent a two-parameter function, with t_0 set to 0, to allow for a comparison of growth rates between time periods. For *R. aurorubens*, the 1985–93 and 1979–81 curves are modified from Zhao et al. (1997). For *P. pagrus*, curves from 1979–81 and 1988–90 are modified from Harris and McGovern (1997), and for *M. phenax* curves from 1979–89 and 1990–97 are modified from Harris et al (2002). The dashed line in each graph represents the minimum size limit for that species.

Scamp

Scamp were classified as experiencing overfishing through a population study in 1998 (Manooch et al., 1998), and this has remained the official NMFS status (NMFS, 2010). Scamp have been managed with a commercial 20 inch TL (471 mm FL) minimum size limit since 1992. There have been no other commercial regulations for this species until recently when a seasonal closure (January through April) was implemented to protect the species during their spawning season.

In contrast to red porgy and vermilion snapper, legal-size scamp comprised almost entirely older fish. This finding indicates that the commercial catches are not retaining a high proportion of fast growing phenotypes (young, but large fish). Sublegal- and legal-size scamp had minimal overlap in age ranges with mean ages differing by more than three years. Ages 5 and under were predominately sublegal-size fish, and nearly all immature scamp were sublegal size and female (Fig. 2; Tables 3 and 4). Size and age at maturation and transition are similar to values from the 1970s through the 1990s (Harris et al., 2002), indicating that scamp are not undergoing increased fishing mortalities and that minimum size limits are an effective management tool for scamp. Comparisons of von Bertalanffy curves from previous studies (Matheson et al., 1986; Harris et al., 2002) show similar growth rates and asymptotic lengths (Fig. 4C). Furthermore, since the 1992 minimum size limit regulation, landings, although variable, have shown no in-

[2] SAFMC (South Atlantic Fishery Management Council). 2008. Final, amendment number 15B to the fishery management plan for the snapper grouper fishery of the South Atlantic region, 159 p. + appendices. South Atlantic Fishery Management Council, One Southpark Circle, Suite 306, Charleston, SC 29407.

Table 5

Summary of the commercial fishing regulations mandated by the South Atlantic Fishery Management Council that have affected the snapper-grouper complex. TL=total length, t=metric ton. Amend.=amendment.

Year	Species	Regulation
1983 (Amend. 1)	Snapper-Grouper complex	Trawls were required to have a 4-inch (10-cm) mesh size.
1992 (Amend. 4)	Snapper-Grouper complex	Trawls were banned
1998 (Amend. 8)	Vermilion snapper	12-inch (30-mm) TL minimum size limit
	Red porgy	12-inch (305-mm) TL minimum size limit
	Scamp	20-inch (508-mm) TL minimum size limit
1999 (Amend. 9)	Red porgy	14-inch (356-mm) TL minimum size limit; Mar–Apr closure
1999–2000	Red porgy	Emergency interim ruling: No landings Sep 1999–Aug 2000
2000 (Amend. 12)	Red porgy	50 lb/trip (23 kg/trip) limit May–Dec and a Jan–Apr closure
2006 (Amend. 13C)	Vermilion snapper	11,000,000 lb (5000 t) quota (gutted fish)
	Red porgy	127,000 lb (58 t) quota (gutted fish); 120 fish/trip limit from May to Dec
2009 (Amend. 16)	Vermilion snapper	Jan–Jun: 315,523 lb (143 t) quota (gutted fish); Jul–Dec: 302,523 lb (137 t) quota (gutted fish)
	Scamp	Jan–Apr closure for scamp (beginning in 2010)

creasing trend. Current size regulations (471 mm FL) restrict the removal of scamp to large mature females and males. Scamp spawn as small as 289 mm FL (Harris et al., 2002), providing ample time for both young and old females to have multiple reproductive seasons before being removed by the fishery.

One note of concern is the continual decrease in the number of males. Harris et al. (2002) noted a decrease in the number of males from 1979–89 to 1990–97, from 34% to 21%, and Coleman et al. (1996) in the Gulf of Mexico noted a decrease over 20 years from 36% to 18%. Males have continued to decline to the 12% found in our study. The limited number of transitioning and male scamp are of concern, because this may be an indication of sperm limitation. Comparing our age and size of transition to those determined by Allsop and West (2003), we found that our age of transition is much higher than expected, but the size of transition (based on the FL_{max} in this study) is similar to the expected value. The age at transition may be higher than that estimated in Allsop and West (2003) because it is thought that sexual transition in scamp is socially mediated within post-spawning aggregations (Harris et al., 2002), thereby limiting transition in both time and space. Simply increasing the minimum size limit may not reverse this trend because more females will survive but may not transition to males, thereby further skewing the sex ratio (Heppell et al., 2006). A management regime that protects males and preserves the sex ratio is needed. Year round deep water area closures or marine protected areas would work best to preserve the expected sex ratios, as these closures would protect males as shown by Heppell et al.'s model (2006). An alternative hypothesis to explain the lack of male specimens in our study is the segregation of males from females in time and space as is seen in gag (*Mycteroperca microlepis*) (Coleman and Koening, as cited in Heppell et al., 2006). Current data do not allow us to test these hypotheses, but conservative management is needed to protect males in locations where scamp is known to occur.

Conclusions

This study indicates strongly that heavily exploited fish stocks (those being overfished or in the state of having been overfished) managed by minimum size limits can create populations with many small, old fish through the disproportional removal of the large, young fish (fast growing phenotype). Which stocks are affected would depend on the selected minimum size limit and the specific life histories of that stock. The two species undergoing heavy exploitation, vermilion snapper (experiencing overfishing) and red porgy (overfished), both showed signs that the fishery was landing many young, large fish (fast growing phenotypes). For both species, growth has increased from historical periods, and asymptotic length is near the minimum size limit. Additional factors that may be influencing these changes are gear type and gear selectivity because the past fishery was primarily a trawling fishery, whereas the current fishery is a hook-and-line industry. For scamp, the species not experiencing overfishing (overfished status unknown), there were few young large fish captured, and growth rate and asymptotic length were similar to those of other time periods.

Our study shows that the hook-and-line fishery targets young, but large fish with a fast growing phenotype. These fast growing phenotypes often have an associated bold and aggressive behavior and are caught more often than their counterparts, the slow growing

phenotypes (Biro and Post, 2008). Although growth rates have increased for both vermilion snapper and red porgy, it is interesting to note that asymptotic lengths are only slightly greater than the minimum size limits. Because this increased growth rate is not seen in fish larger than the minimum size limit, this finding may imply that the portion of the population that is larger than the minimum size limit consists of more slow growing phenotypes.

Conover and Baumann (2009) noted that after removing a minimum size limit regulation, even if the shift in the population's size-at-age was due solely to phenotypic plasticity, the population had not regained its previous size-at-age distribution after four generations. In fish such as snappers and groupers, which have long generation times, it could take many decades before a recovery is seen. Managers need to consider the life history characteristics of each species in light of its susceptibility to phenotypic shifts due to minimum size limits. Therefore, in a multispecies industry where species-specific minimum size limits are aiding in a shift to smaller sizes at age, an ecosystem-based management plan that includes a multispecies quota system is a good precautionary approach to maintaining a sustainable fishery.

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Literature cited

Allman, R. J.
2007. Small-scale spatial variation in the population structure of vermilion snapper (*Rhomboplites aurorubens*) from the northeast Gulf of Mexico. Fish. Res. 88:88–99.

Allsop, D. J., and S. A. West.
2003. Constant relative age and size at sex change for sequentially hermaphroditic fish. J. Evol. Biol. 16:921–929.

Biro, P. A., and J. R. Post.
2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Natl. Acad. Sci. U.S.A. 105:2919–2922.

Buckley, L. J., A. S. Smigielski, T. A. Halavik, E. M. Caldarone, B. R. Burns, and G. C. Laurence.
1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. Mar. Ecol. Prog. Ser. 74:125–135.

Coleman, F. C., C. C. Koenig, and L. A. Collins.
1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environ. Biol. Fishes 47:129–141.

Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, R. W. Chapman, G. R. Sedberry, and C. B. Grimes.
2000. Long-lived reef fishes: the grouper-snapper complex. Fisheries 25:14–21.

Conover, D. O., S. A. Arnott, M. R. Walsh, and S. B. Munch.
2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). Can. J. Fish. Aquat. Sci. 62:730–737.

Conover, D. O., and H. Baumann.
2009. The role of experiments in understanding fishery-induced evolution. Evol. Appl. 2:276–290.

Conover, D. O., and S. B. Munch.
2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.

Cuellar, N., G. R. Sedberry, and D. M. Wyanski.
1996. Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States. Fish. Bull. 94:635–653.

Daniels, E. A.
2003. Sexual maturity, spawning dynamics, and fecundity of red porgy, *Pagrus pagrus*, off the southeastern United States. M.S. thesis, 78 p. Univ. Charleston, Charleston, SC.

DeVries, D. A.
2006. No evidence of bias from fish behavior in the selectivity of size and sex of the protogynous red porgy (*Pagrus pagrus*, Sparidae) by hook-and-line gear. Fish. Bull. 105:582–587.

Goodyear, C. P.
1996. Minimum sizes for red grouper: Consequences of considering variable size at age. N. Am. J. Fish. Manage. 16:505–511.

Grift, R. E., A. D. Rijnsdorp, S. Barot, M. Heino, and U. Dieckmann.
2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. 257:247–257.

Harris, P. J.
2003. Age, growth and reproductive biology of the red porty, *Pagrus pagrus*, from the southeastern United States, 1995–2002, 41 p. South Caroline Dept. Natural Resources, Charleston, SC.

Harris, P. J., and J. C. McGovern.
1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994. Fish. Bull. 95:732–747.

Harris, P. J., S. M. Padgett, and P. T. Powers
2001. Exploitation-related changes in the growth and reproduction of tilefish and the implications for the management of deepwater fisheries. *In* Island in the stream: oceanography and fisheries of the Charleston Bump (G. R. Sedberry, ed.), p. 199–209. Am. Fish. Soc., Bethesda, MD.

Harris, P. J., D. M. Wyanski, D. B. White, and J. L. Moore.
2002. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern north Atlantic, 1979–1997. Bull. Mar. Sci. 70:113–132.

Heino, M., and O. R. Godø.
2002. Fisheries-induced selection pressures in the

context of sustainable fisheries. Bull. Mar. Sci. 70: 639–656.

Heppell, S. S., S. A. Heppell, F. C. Coleman, and C. C. Koenig.
2006. Models to compare management options for a protogynous fish. Ecol. Appl. 16:238–249.

Hood, P. B., and A. K. Johnson.
1999. Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. Fish. Bull. 97:828–841.

Hood, P. B., and A. K. Johnson.
2000. Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico. Fish. Bull. 98:723–735.

Hutchings, J. A.
2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. 62:824–832.

Hutchings, J. A., and R. A. Meyers.
1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 50:2468–2474.

Kjesbu, O. S., P. Solemdal, P. Bratland, and M. Fonn.
1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 53:610–620.

Kuparinen, A., and J. Merilä.
2007. Detecting and managing fisheries-induced evolution. Trends Ecol. Evol. 22:652–659.

Law, R.
2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57:659–668.

Liu, M., and Y. Sadovy.
2004. The influence of social factors on adult sex change and juvenile sexual differentiation in a diandric, protogynous epinepheline, *Cephalopholis boenak* (Pisces, Serranidae). J. Zool. 264:239–248.

Manooch, C. S., III, and G. R. Huntsman.
1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26–33.

Manooch, C. S., III, J. C. Potts, M. L. Burton, and P. J. Harris.
1998. Population assessment of the scamp, *Mycteroperca phenax*, from the southeastern United States. NOAA Tech. Memo. NMFS-SEFSC-410, 57 p.

Matheson, R. H., III, G. R. Huntsman, and C. S. I. Manooch.
1986. Age, growth, mortality, food and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38:300–312.

Mollet, F. M., S. B. M. Kraak, and A. D. Rijnsdorp.
2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. Mar. Ecol. Prog. Ser. 351:189–199.

Munday, P. L., P. M. Buston, and R. R. Warner.
2006a. Diversity and flexibility of sex-change strategies in animals. Trends Ecol. Evol. 21:89–95.

Munday, P. L., J. W. White, and R. R. Warner.
2006b. A social basis for the development of primary males in a sex-changing fish. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 273:2845–2851.

NMFS (National Marine Fisheries Service).
2010. 2009 status of U.S. fisheries, 28 p. U.S. Dept. Comm., NOAA, National Marine Fisheries Service, Silver Spring, MD. [Available at http://www.nmfs.noaa.gov/sfa/statusoffisheries/SOSmain.htm (accessed April 2011).]

Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey, and U. Dieckmann.
2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 62:811–823.

Pitcher, T. J., and P. J. B. Hart.
1982. Fisheries ecology, 414 p. Croom Helm, London.

Potts, J. C., and C. S. Manooch, III.
2002. Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters. Fish. Bull. 100:81–89.

Ratner, S., and R. Lande.
2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. Ecology 82:3093–3104.

Reznick, D. A., H. Bryga, and J. A. Endler.
1990. Experimentally induced life-history evolution in a natural population. Nature 346:357–359.

Reznick, D. N., and C. K. Ghalambor.
2005. Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 62:791–801.

Ricker, W. E.
1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia 1945:84–94.

Rothschild, B. J.
1986. Dynamics of marine fish populations, 277 p. Harvard Univ. Press, Cambridge, MA.

SAFMC (South Atlantic Fishery Management Council).
1983. Fishery management plan, regulatory impact review, and final environmental impact statement for the snapper-grouper fishery of the south atlantic region, 303 p. SAFMC, Charleston, SC.

Schmidt, D. J., M. R. Collins, and D. M. Wyanski.
1993. Age, growth, maturity, and spawning of Spanish mackerel, *Scomberomorus maculatus* (Mitchili), from the Atlantic coast of the southeastern United States. Fish. Bull. 91:526–533.

SEDAR (SouthEast Data, Assessment, and Review).
2006. SEDAR-01 Update: Stock assessment of red porgy off the southeastern United States, SEDAR update assessment, 152 p. South Atlantic Fishery Management Council, Beaufort, NC. [Available at http://www.sefsc.noaa.gov/sedar (accessed April 2011).]

SEDAR (SouthEast Data, Assessment, and Review).
2008. SEDAR-17: Stock assessment report: South Atlantic vermilion snapper, 450 p. South Atlantic Fishery Management Council, Charleston, SC. [Available at http://www.sefsc.noaa.gov/sedar (accessed April 2011).]

Sharpe, D. M. T., and A. P. Hendry.
2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol. Appl. 2:260–275.

Stephen, J. A., and P. J. Harris.
2010. Commercial catch composition with discard and immediate release mortality proportions off the southeastern coast of the United States. Fish. Res. 103:18–24.

Stokes, K., and R. Law.
2000. Fishing as an evolutionary force. Mar. Ecol. Prog. Ser. 208:307–309.

Swain, D. P., A. F. Sinclair, and J. M. Hanson.
2007. Evolutionary response to size-selective mortality in an exploited fish population. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 274:1015–1022.

Trippel, E. A., O. S. Kjesbu, and P. Solemdal
1997. Effects of adult age and size structure on reproductive output in marine fishes. *In* Early life history

and recruitment in fish populations (R. C. Chambers, and E. A. Trippel, eds.), p. 31–62. Chapman & Hall, New York.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover.
2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecol. Lett. 9:142–148.

Williams, E. H., and K. W. Shertzer.
2005. Effects of fishing on growth traits: a simulation analysis. Fish. Bull. 103:392–403.

Wyanski, D. M., D. B. White, and C. A. Barans.
2000. Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus,* off North Carolina and South Carolina. Fish. Bull. 98:199–218.

Zhao, B., and J. C. McGovern.
1997. Temporal variation in sexual maturity and gear-specific sex ratio of the vermilion snapper, *Rhomboplites aurorubens,* in the South Atlantic Bight. Fish. Bull. 95:837–848.

Zhao, B., J. C. McGovern, and P. J. Harris.
1997. Age, growth and temporal changes in size at age of the vermilion snapper from the South Atlantic Bight. Trans. Am. Fish. Soc. 126:181–193.

Distribution patterns of tidepool fishes on a tropical flat reef

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Abstract—Rockpools on a tropical flat reef off the southeastern coast of Brazil were sampled to determine the influence of pool morphometry and water characteristics on fish community structure. The pool closest to the inner fringe of the reef had lower salinity and higher temperature due to inflow of groundwater. The other pools varied only with respect to their morphometric characteristics, algal cover, and bottom composition. Species with a strong affinity for estuarine-like waters characterized the pool closest to the beach and distinguished its fish community from that of the other pools. Instead of being strongly structured by the physicochemical setting and position in the reef, fish communities of the other pools were determined by behavioral preferences and intra- and interspecific interactions. Differences in community structure were related to pool size (the larger sizes permitting the permanency of schooling species), to algal cover (which allowed camouflage for large predatory species), to bottom composition (which provided substrate for turf flora available to territorial herbivores), and to ecological effects (e.g., competition, territoriality, and predation). Although distribution patterns of tidepool fishes have previously been related to the availability of niches, independent of pool position in the reef, our results show synergistic interactions between water properties, presence or absence of niches, and ecological relationships in structuring tidepool fish communities.

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Habitually, at low tide most fishes of the intertidal zone are concentrated in tidepools. There, physicochemical (e.g., temperature and salinity) and biological (e.g., recruitment) variables are inherently related to the duration of pool isolation from the sea (Gibson, 1986). Thus, isolation has been suggested to be a determinant for the establishment and maintenance of a fish community (e.g., Gibson, 1972) and has become one of the "templates" onto which fish distribution patterns are established, either partially or totally (Zander et al., 1999). However, factors such as surface area or water volume also influence community composition and structure (Mahon and Mahon, 1994). For instance, larger, deeper pools allow the permanency of more stenotopic species (Gibson and Yoshiyama, 1999). Therefore, the distribution of fishes is to some extent "azonal" (i.e., pool height within the intertidal zone is not necessarily the single or even the main determinant for fish distribution) because the occurrence of each species is more dependent upon pool characteristics than upon the vertical position of the pool on the rocky shore (Zander et al., 1999). On the other hand, the synergistic effects between pool morphometry and pool isolation have obscured the distinction of their respective contributions to the spatial distribution of fishes (Bennett and Griffiths, 1984). As a consequence, the influence of ecological aspects like competition, predation, or niche availability on shaping tidepool fish distributions may thus far be inadequately evaluated (Faria and Almada, 2001, 2006; Arakaki and Tokeshi, 2010; Rojas and Ojeda, 2010).

In flat reefs, there are no significant differences in vertical position of pools and in wave impact on pools and, consequentially, the duration of isolation from the sea is similar for all pools (e.g., Mahon and Mahon, 1994). In such a situation, pool morphometry probably is the most influential factor on the distribution of fishes. The relative evenness of physicochemical factors among pools enables a standardization of the species filter (i.e., one or more environmental factors that impede species occurrence), and differences among pools will be due more to differences in the availability of resources (e.g., food, mates, space, protection) and microhabitat. However, despite offering an opportunity to study these effects without overly confounding factors, flat reef areas have been little studied in respect to the spatial distribution of their intertidal fishes (Mahon and Mahon, 1994; Zander et al., 1999). Thus, how pool size and shape (depth and volume) and substrate complexity interact to affect community composition remains poorly understood. Therefore, our objectives were to investigate the effects of the physicochemical setting (temperature and salinity) and morphometric characteristics of pools on the structure of fish communities on a flat reef, without the interactive effects caused by differences in the duration of isolation of the rockpools. In comparison with a "classic" rocky shore (with varying duration of isola-

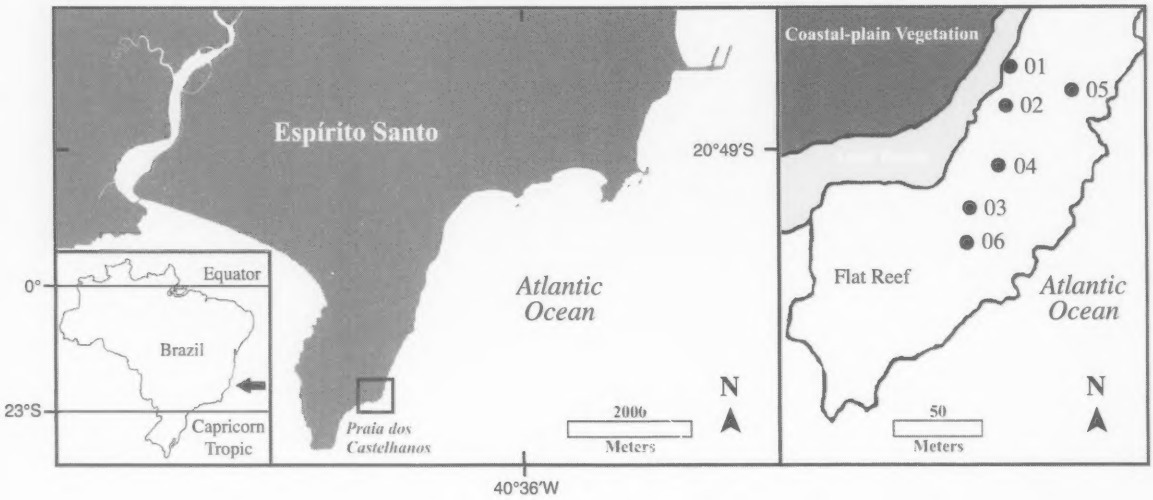

Figure 1

Location of study area (Praia dos Castelhanos) off the coast of Espírito Santo, Brazil. The spatial distribution of the rockpools on the reef flat is shown in the map on the right.

tion from the sea; e.g., Gibson, 1972), the abundance and distribution of fishes on a flat reef are expected to be affected by less complex interactions between environmental and ecological variables and that there would be a lower disparity in fish community structure among pools. Such natural simplification of environmental complexity could also shed some light on how the current tendency of habitat homogenization driven by modern anthropogenic activities (Thompson et al., 2002) may affect the divergence of fish communities (Villéger et al., 2010).

Materials and methods

Study area

The study was conducted at Praia dos Castelhanos (20°49′S, 40°36′W), in the state of Espírito Santo in southeastern Brazil (Fig. 1). The mean water level relative to the reference datum of zero-level of Brazilian marine charts is 0.82 m. The reef is a complex of carbonate material composed of encrusting coralline algae and stony coral skeletons with sparse lateritic (ferruginous) rocks and is essentially flat. During the ebb tide a large number of pools become isolated. Pool substrates often consist of sand and gravel and pool walls are characteristically irregular, almost vertical, and are covered by algal turf, soft macro-algae, crustose coralline algae, encrusting soft-coral, and a few stony corals.

Morphological characterizations of tidepools

Six isolated tidepools (without connectivity to the sea or other pools during the ebb tide) were selected: two located near the sand beach (pools 1 and 2), two in an intermediary position (pools 3 and 4), and two closer to the water edge (pools 5 and 6; Fig. 1). The mean time of exposure to air was about three hours per day. The height of the reef flat was located at about 6 cm (pool 2), 11 cm (pool 3), 10 cm (pool 4), 20 cm (pool 5), and 13 cm (pool 6), below that near pool 1. The pools were characterized on a single occasion relative to their surface area, depth, and bottom rugosity. Surface area was estimated by using a 3×1-m grid of 10×10-cm squares. Depth was measured with a ruler at randomly chosen intersections of the grid. Volume was derived from surface area and mean depth. Rugosity was measured by the chain-and-tape technique (Wilding et al., 2010).

Sampling

Sampling was conducted every three months between August 2005 and June 2007 (n=8) during the mornings of two consecutive days. During the first day, water temperature and salinity were measured with a mercury thermometer (0.5°C precision) and a refractometer (1 psu precision). Measurements were taken at three separate times in each pool: immediately after isolation of the pool from the sea ("beginning"); when the water level fell below reef level ("middle"); and at the time corresponding to the lowest level of the tide and immediately before the pool was connected to the rising sea ("end"). Algal cover and bottom composition were visually estimated on a scale ranging between 0 and 100 (Bennett and Griffiths, 1984). Algal cover was estimated only for pool walls and consolidated bottom areas and refers exclusively to macroalgae. Substrate types were categorized as sand (less than 1 mm diameter), gravel, or rock (diameter greater than 50 mm), and the sum of all categories

Table 1

Morphometric characteristics, substrate composition, macroalgae cover, and physicochemical parameters of pools at Praia dos Castelhanos, Espírito Santo, Brazil. Pools were characterized once for depth, surface area, volume, and rugosity and every three months between August 2005 and June 2007 for substrate, cover, and physicochemical parameters (n=8 for all pools except pool 1 where n=7). *=mean (range: minimum–maximum). Depth (max)=mean depth (and maximum depth); area=surface area; vol.=volume; rug.=rugosity.

	Morphometric characteristics				Substrate			Cover	Physico-chemical parameters	
Pool	Depth (max.) cm	Area m^2	Vol. m^3	Rug.	Sand %	Gravel %	Rock %	Algae %	Temperature* °C	Salinity*
1	8.30 (20.5)	6.35	0.53	1.11	30	10	60	20	26.1 (22.5-35.0)	28.1 (17.0–35.8)
2	22.2 (36.3)	10.15	2.24	1.19	80	10	10	40	24.4 (21.5–29.6)	34.3 (32.0–38.0)
3	17.4 (25.5)	1.36	0.24	1.26	30	60	10	40	24.8 (22.0–30.1)	34.3 (31.4–37.0)
4	28.2 (49.0)	7.88	2.22	1.30	40	20	40	70	24.2 (21.8–29.7)	34.5 (32.0–37.0)
5	23.8 (46.0)	16.12	3.81	1.20	10	10	80	30	24.7 (22.2–28.0)	34.8 (31.3–39.0)
6	25.6 (51.0)	6.52	1.67	1.27	20	50	30	40	24.5 (22.2–24.9)	34.7 (31.0–38.0)

corresponded to 100% of bottom cover. The ichthyofauna was collected on the second sampling day with hand nets and with application of water-based rotenone solution (Polivka and Chotkowski, 1998; Gibson, 1999) and was later fixed in 10% formalin. Due to seasonal variation in beach profile, tidepool 1 was covered by sand during the August 2006 sampling.

Sample processing

The fishes were measured (total length; TL) to the nearest mm and weighed (individual total wet weight; W) at 0.01 g precision. The species were categorized by their degree of residency in pool habitats (modified from Griffiths, 2003) as permanent residents, opportunists, and transients. Permanent residents (PR) can spend their entire life in pools and are frequently highly adapted for intertidal life. Opportunists (O) spend only part of their life history in pools, usually as juveniles or during high tide feeding excursions, when they are trapped in pools. Transients (T) are species that only occasionally or accidentally enter pools, generally have no specialized adaptations for intertidal life, and normally occur in large rockpools for a short period of time (from a tidal cycle to several weeks). In this study, the assignment of species to categories was based upon frequency of capture, life stage(s) present in pools, species size, and occurrence in the infralittoral zone.

Data analysis

Temperature and salinity data were tested for normality by the Kolmogorov-Smirnov-Lilliefors test (Zar, 1999) and the data were shown to be normally distributed (P>0.05). Variation in temperature and salinity during the ebb tide was tested though repeated-measures ANOVA (n=8; except n=7 for tidepool 1), and contrasts of "beginning vs. middle" and "beginning vs. end" were tested. The Mauchly test was used to verify data sphericity and the F-value obtained from the Greenhouse-Geisser test was used when sphericity assumptions were violated. The fish community of each pool was described by the mean number of individuals, number of taxa, Shannon-Wiener index (using $\log_e$), and Pielou's evenness. Friedman nonparametric tests were used to detect differences among pools with significance estimated through Monte Carlo resampling (10,000 runs) (Zar, 1999). The mean length and weight of all individuals were tested among pools by using Kruskal-Wallis nonparametric tests for independent samples with Monte Carlo resampling (10,000 runs).

Nonmetric multidimensional scaling (nMDS) was used to determine the similarity between rockpools by using 1) the morphometric characteristics (4 variables [area, mean depth, volume, rugosity]×6 pools), 2) the physicochemical parameters of the water (6 variables [mean, minimum and maximum for temperature and salinity]×6 pools), and 3) the fish community structure (64 variables [=taxa]×6 pools) by using total abundance and total weight (summed up across the eight sampling events). Data were transformed (fourthth root) and matrices were built with the Bray-Curtis coefficient.

Results

Characteristics of rockpools

The pools differed in morphometric characteristics but were similar in their physicochemical setting, except for pool 1 (Table 1). Changes during low tide were exacerbated in pool 1 (Fig. 2) because of groundwater inflows (which lowered salinity during the rainy season) and shallowness (which allowed temperature to rise because of the high ratio between area [i.e., insolation] and volume). In extreme cases, a thermopycnocline formed within the pool (without apparent effect on the ichthyofauna; senior author, personal observ.). Besides

being segregated by its physicochemical characteristics (Fig. 3B), pool 1 also differed from other pools (Fig. 3A; Table 1) on account of the smoothness of its bottom. This feature is probably caused by high hydrodynamics and the constant sanding of the rocky substratum by virtue of the pool location in the breaker zone adjacent to the beach. Abrasion also severely limited growth of macroalgae and sessile invertebrates (Table 1). The five other pools separated into three categories: category 1 consisted of pool 3 (very small and filled with gravel), category 2 consisted of pool 5 (of large size with high rock and low sand covers), and category 3 consisted of the remaining pools 2, 4, and 6. The sandiness of pool 2, the depth, rugosity, algal and sand cover of pool 4, and the "graveliness" (coarseness of unconsolidated substrate) of pool 6 were insufficient to differentiate them (Fig. 3A).

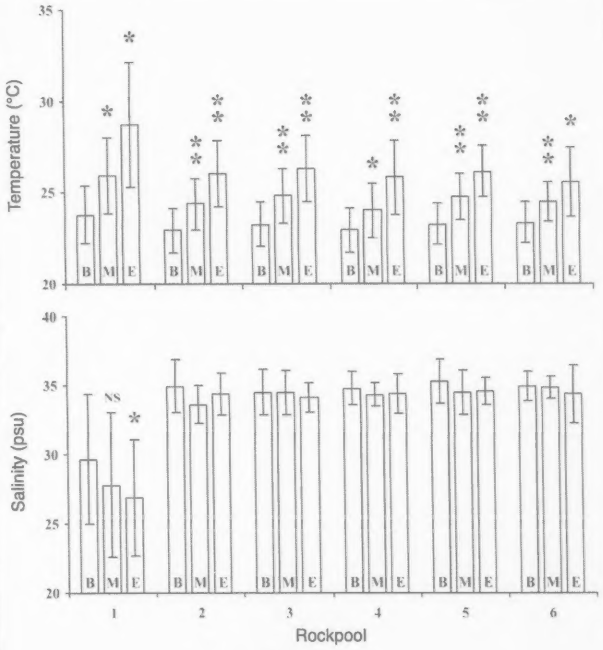

Figure 2

Mean (±1 standard deviation) temperature and salinity at the beginning (B), middle (M), and end (E) of isolation of pools from the sea at Praia dos Castelhanos, Espírito Santo, Brazil. Differences in these variables during the period of pool exposure to air were tested by repeated-measure ANOVA models with the Greenhouse-Geisser test (temperature in pools 2, 3, and 5) or the sphericity assumed test (all other models). In significant models (temperature for all pools, with $P \leq 0.001$; salinity in pool 1 with $P \leq 0.05$), results for contrast tests between the beginning and middle periods and the beginning and end periods are indicated above M and E, respectively. For all pools, $n=8$ except for pool 1, where $n=7$. NS=not significant; *=$P \leq 0.01$, **=$P \leq 0.001$.

Spatial distribution of fishes

A total of 3448 individuals, representing 64 taxa (58 species) and 27 families, was caught (Table 2). Sixteen of the 58 species, representing 64% of the total number of individuals, were considered permanent residents (PR), 19 (28%) were opportunists (O), and 23 (7.3%) were transients (T). Abundance, richness, diversity, and total wet weight of all fish differed among rockpools, but there were no significant differences in Pielou's evenness or mean length (Fig. 4). Abundance was very high at pool 5 due to *Halichoeres poeyi*, *Stegastes fuscus*, and *Acanthurus bahianus*. Individual mean weight was very high at pool 4 because of rather large and abundant *Labrisomus nuchipinnis* and juveniles of *Sparisoma axillare*. The community indices for pool 1 were characteristic of environments with elevated stress level (e.g., estuaries): high abundance, low diversity, and dominance of few species. Permanent residents were the most representative pool users (above 40% of total) in both number and weight. Proportions of the three user categories varied among pools. Pools 1 to 4 were dominated by permanent residents (above 60% in number and above 80% in weight). In pools 5 and 6 (and in a smaller measure, 2 and 4), although permanent residents remained dominant, the number and weight of opportunists and transients were very representative (Fig. 5).

The ten most-abundant species were either permanent residents or opportunists and showed four different patterns of spatial distribution (Friedman test, Fig. 6). Pattern A, where species were most abundant at pool 5 and rare elsewhere (except pool 6), was displayed by *A. bahianus*, *H. poeyi*, and *S. fuscus*. Species most abundant at pool 1 but rare in other pools, *Bathygobius soporator* and *Ctenogobius boleosoma*, were classified as displaying pattern B. Absence at pool 1 and low abundance at pool 3, as for *Malacoctenus delalandei* and *S. axillare*, characterized pattern C. The most abundant species overall, *Bathygobius mystacium* and *L. nuchipinnis*, displayed pattern D where abundance was most expressive at pool 5 but remained relatively high in the other pools. No obvious pattern of spatial distribution was identified for *Abudefduf saxatilis*. Except for *B. soporator* and *C. boleosoma* (pattern B), there was no similarity between abundance and physicochemical characteristics of rockpools. The distribution patterns of mean individual weight (not shown) of these most-abundant species did not present much similarity with those of abundance (Fig. 6). The gobies *C. boleosoma* and (to a lesser degree) *B. mystacium* showed a pattern similar to pattern B detected for abundance. The mean individual weight of *Abudefduf saxatilis* was higher in larger pools (2 and 5) and that of *B. soporator* was lowest in pool 1 which presented the highest abundance. Overall, six of the ten species displayed significant differences in

weight among pools (*B. mystacium*, *L. nuchipinnis*, *C. boleosoma*, *A. saxatilis*, *S. fuscus*, and *A. bahianus*).

The nMDS ordination analysis on both abundance and mean weight showed that the fish assemblage, when all taxa are considered, is structured differently among pools (Fig. 7). In both cases, pools 1 and 3 were segregated from all others (and each other), 3 because of a low total abundance and a low number of taxa and 1 because of the absence of some common species (*H. poeyi*, *S. axillare*, and *M. delalandei*) and the dominance of *B. soporator* and *C. boleosoma*. The other pools, loosely grouped, shared similar values in number of taxa, Shannon-Weiner diversity, total length (Fig. 4), and higher percentages of opportunist and transitory species (Fig. 5). Although differences in the physicochemical setting of pools were low (except for pool 1), the 10 most abundant taxa presented distinctive distribution patterns for abundance related to the morphometric characteristics of each pool, such as position on the reef, depth, surface area, volume, substrate composition, algal cover and rugosity.

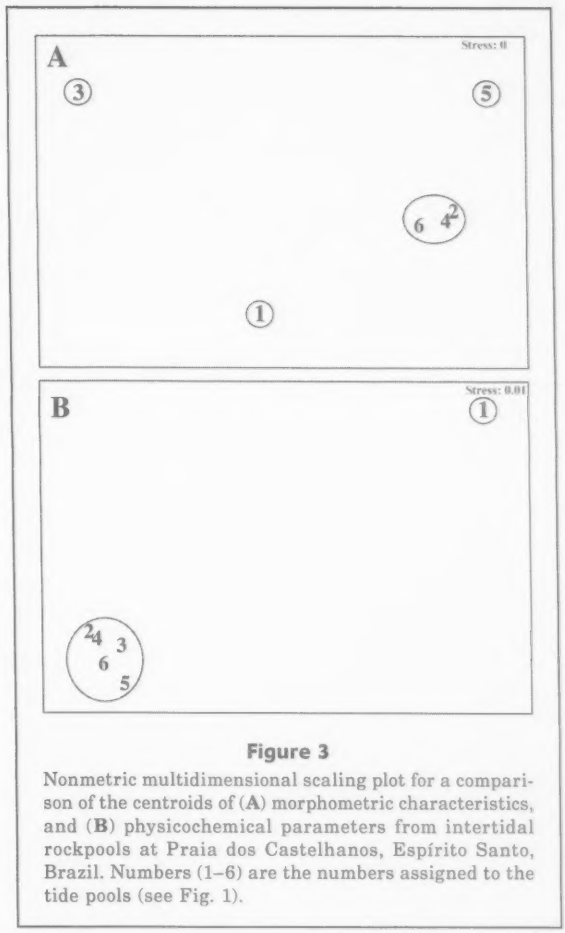

Figure 3

Nonmetric multidimensional scaling plot for a comparison of the centroids of (**A**) morphometric characteristics, and (**B**) physicochemical parameters from intertidal rockpools at Praia dos Castelhanos, Espírito Santo, Brazil. Numbers (1–6) are the numbers assigned to the tide pools (see Fig. 1).

Discussion

Spatial distribution of fishes

Species living in intertidal ecosystems are distributed along a vertical gradient according to their tolerance of physical factors and their response to ecological interactions (Raffaelli and Hawkins, 1996). Although the vertical distribution of sessile organisms has been studied for many years, the distribution of fishes and other mobile organisms that take refuge in pools has not been investigated as extensively because it is much more dynamic and thus more difficult to study (Zander et al., 1999; Thompson et al., 2002). The shape and volume of a pool, its degree of isolation from the sea, and its connectivity with other pools determine the amplitude of the fluctuation in physicochemical characteristics of the water (Mahon and Mahon, 1994; Davis, 2000; Castellanos-Galindo et al., 2005). Consequently, the occurrence of each species is dependent more upon pool characteristics than upon vertical position of the pool on the rocky shore, i.e., species occurrence is nearly azonal (Zander et al., 1999). Other factors, such as exposure to waves (Gibson, 1972; Grossman, 1982) and algal cover (Bennett and Griffiths, 1984), have been investigated, but their influence on the distribution of fishes may be secondary.

Habitat heterogeneity is intimately associated with variability in microhabitats and therefore offers the conditions for the coexistence of antagonistic species (Rojas and Ojeda, 2010). Two main microhabitats are available to rockpool fishes (Griffiths et al., 2006): the substratum of the pool where fish can hide and the complex macroalgal cover used by midwater or pelagic species. Rojas and Ojeda (2010) demonstrated that small fishes prefer pools of low structural complexity where there are fewer ambush areas for predators. On the other hand, fish distribution on a rocky shore is also affected by inter-intra specific interactions such as competition and predation (Gibson and Yoshiyama, 1999; Zander et al., 1999) that may lead to microhabitat segregation (Faria and Almada, 2001). Thus, many different physical and ecological factors regulate the distribution and structure of fish community in rockpools (e.g., Gibson, 1972, 1982), and the principal difficulty is to determine the respective contribution of each of these.

There are about three "vertical" ecological pool-zones on a flat, fringing, intertidal rocky reef. The first is located at and just below the upper edge of the reef. This is an area under stronger atmospheric and terrestrial influence and that is subject to shifting conditions from reef to nonreef environment. Permanent residents and a few opportunistic fish that can tolerate the physiologic stress caused by physicochemical changes during the exposure of the reef to the air (Evans et al., 1999), normally dominate this zone. There, B-pattern species, such as the eurythermic and euryhaline *B. soporator* and *C. boleosoma*, probably find resources available and lower predation risk because at low tide

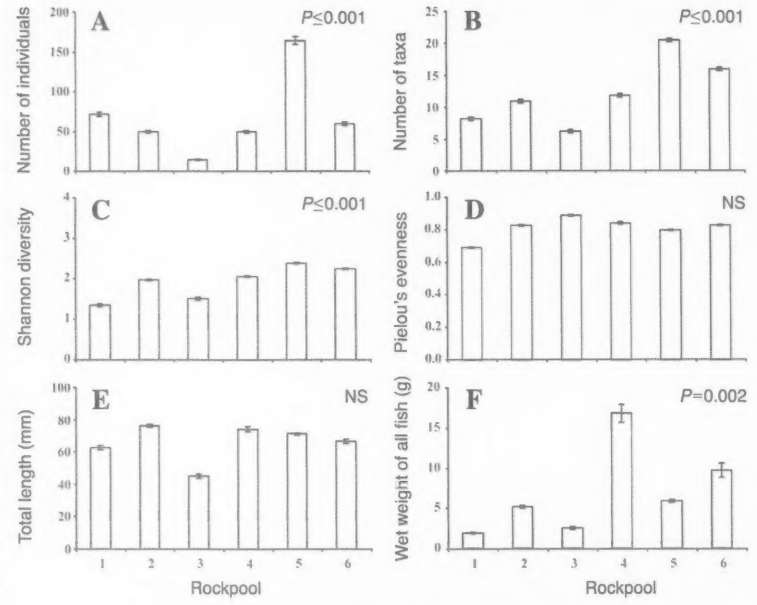

Figure 4

Mean (±1 standard error) of (**A**) number of individuals, (**B**) number of taxa, (**C**) Shannon diversity, (**D**) Pielou's evenness, (**E**) total length, and (**F**) total wet weight of all fish. The results of the Friedman (A–D) or Kruskal-Wallis (E–F) tests for differences among pools are inserted in the graphs. n=8; NS=not significant.

the number of interspecific competitors and predators also is regulated by physiologic stress. Moreover, equivalent-size pools at the reef's higher fringe hold more individuals than those at lower levels because of the overwhelming numerical dominance of thermal and saline stress-adapted species. In that case, low substrate heterogeneity and environmental complexity, held as important factors for community structuring, do not necessarily translate into low fish abundance as commonly thought (Griffiths et al., 2006). Immediately below this upper zone, the middle zone is much less affected by external influences (e.g., groundwater seepage) and consequently even small pools present less extreme and less stressful conditions. Thus, species with little or no adaptation to intertidal life (opportunistic and transient fish) are more common in this zone and differences in fish community structure among pools would be directly related to pool morphometry because it will determine the number of available niches. The last zone (unstudied) is close to the sea, and a high number of pools, if not all, are extensively connected to it through a pipe and cave system; at low tide, water circulation remains intense in these pools because it is driven by waves on the forereef from a meter to tens of meters away. Occurring in these pools are juveniles and small-size adults of infralittoral species not found elsewhere on the reef flat.

According to Mahon and Mahon (1994), large tidepools have higher numbers of individuals, species richness, and biomass because of higher availability of resources and niches. Such a pattern was clearly distinguishable at Praia dos Castelhanos and presented some interesting twists that shed some light on the mechanisms responsible for pool-specific community structure. Instead of being strongly structured by the physicochemical setting, middle zone communities were finely tuned by minor differences in pool characteristics and ecological effects such as competition, predation, and territorialism. In particular, the abundance of territorial species is related to their need to establish territory and, because larger pools provide more space, they also offer an opportunity for a larger number of territories. Nevertheless, for territorial herbivores (such as *S. fuscus*, pattern A) the ultimate factor is sufficient consolidated substrate in sunlit areas for these species to maintain their "gardens". In a similar way, roving herbivores such as *A. bahianus* (pattern A) are particularly abundant in large pools filled with rocks because schooling behavior (schools usually contain 5–20 individuals) and herbivory create a demand for ample space and adequate substrate (Lawson et al., 1999). Finally, a number of discrete and solitary species, such as the roving herbivore *S. axillare* (pattern C) and the carnivores *L. nuchipinnis* (pattern D) and *M. delalandei* (pattern C),

Table 2

Taxonomic list of individual fish species caught in pools at Praia dos Castelhanos, Espírito Santo, Brazil. Family order follows Nelson (2006). Residency status is adapted from Griffiths (2003): permanent resident (PR), opportunist (O), transient (T), indeterminate (I).

Family and taxa	Residency status
Muraenidae	
Gymnothorax funebris Ranzani, 1840	PR
Gymnothorax moringa (Cuvier, 1829)	PR
Gymnothorax vicinus (Castelnau, 1855)	PR
Ophichthidae	
Ahlia egmontis (Jordan, 1884)	PR
Letharchus aliculatus McCosker, 1974	PR
Myrichthys breviceps (Richardson, 1848)	O
Myrichthys ocellatus (Lesueur, 1825)	O
Myrophis platyrhynchus Breder, 1927	PR
Clupeidae	
Unindentified larvae	I
Ophidiidae	
Raneya brasiliensis (Kaup, 1856)	T
Mugilidae	
Mugil curema Valenciennes, 1836	T
Mugil liza Valenciennes, 1836	T
Atherinopsidae	
Atherinella brasiliensis (Quoy & Gaimard, 1825)	T
Belonidae	
Strongylura timucu (Walbaum, 1792)	T
Syngnathidae	
Bryx dunckeri (Metzelaar, 1919)	T
Micrognathus crinitus (Jenyns, 1842)	T
Scorpaenidae	
Scorpaena plumieri Bloch, 1789	O
Epinephelidae	
Rypticus subbifrenatus Gill, 1861	O
Apogonidae	
Apogon americanus Castelnau, 1855	PR
Phaeoptyx pigmentaria (Poey, 1860)	PR
Carangidae	
Carangoides bartholomaei (Cuvier, 1833)	T
Caranx latus Agassiz, 1831	T
Lutjanidae	
Lutjanus jocu (Bloch & Schneider, 1801)	O
Gerreidae	
Eucinostomus argenteus Baird & Girard, 1855	T
Eucinostomus lefroyi (Goode, 1874)	T
Eucinostomus melanopterus (Bleeker, 1863)	T
Eucinostomus spp. (Unindentified larvae)	I
Haemulidae	
Anisotremus virginicus (Linnaeus, 1758)	T
Haemulon aurolineatum Cuvier, 1830	O
Haemulon parra (Desmarest, 1823)	O
Haemulon plumieri (Lacepède, 1801)	T
Haemulon steindachneri (Jordan & Gilbert, 1882)	T
Sparidae	
Diplodus argenteus (Valenciennes, 1830)	T
Chaetodontidae	
Chaetodon striatus Linnaeus, 1758	O
Pomacentridae	
Abudefduf saxatilis (Linnaeus, 1758)	O
Stegastes fuscus (Cuvier, 1830)	PR
Stegastes variabilis (Castelnau, 1855)	O
Stegastes sp. (Unindentified larvae)	I
Labridae	
Doratonotus megalepis Günther, 1862	O
Halichoeres brasiliensis (Bloch, 1791)	O
Halichoeres poeyi (Steindachner, 1867)	O
Halichoeres sp. (Unindentified larvae)	I
Sparisoma axillare (Steindachner, 1878)	O
Dactyloscopidae	
Dactyloscopus tridigitatus Gill, 1859	T
Blenniidae	
Parablennius marmoreus (Poey, 1875)	T
Scartella cristata (Linnaeus, 1758)	PR
Unindentified blenniid larvae	I
Labrisomidae	
Labrisomus nuchipinnis (Quoy & Gaimard, 1824)	PR
Malacoctenus delalandei (Valenciennes, 1836)	PR
Paraclinus arcanus Guimarães & Bacellar, 2002	T
Gobiesocidae	
Gobiesox barbatulus Starks, 1913	O
Gobiidae	
Barbulifer ceuthoecus (Jordan & Gilbert, 1884)	T
Barbulifer enigmaticus Joyeux, Van Tassell & Macieira, 2009	PR
Bathygobius mystacium Ginsburg, 1947	PR
Bathygobius soporator (Valenciennes, 1837)	PR
Bathygobius sp. (Unindentified larvae)	I
Coryphopterus glaucofraenum Gill, 1863	PR
Ctenogobius boleosoma (Jordan & Gilbert, 1882)	PR
Ctenogobius saepepallens (Gilbert & Randall, 1968)	O
Gobiosoma hemigymnum (Eigenmann & Eigenmann, 1888)	PR
Acanthuridae	
Acanthurus bahianus Castelnau, 1855	O
Acanthurus chirurgus (Bloch, 1787)	O
Paralichthyidae	
Etropus longimanus Norman, 1933	T
Tetraodontidae	
Sphoeroides greeleyi (Gilbert, 1900)	T

heavily rely on crypsis or camouflage provided by macroalgae and on rugosity for either refuge or ambush.

Large pools near the infralittoral are expected to have a larger proportion of transient fishes (Gibson and Yoshiyama, 1999). However, on low gradient reefs, pool size is probably more important than connectivity to the sea or other pools because many such species are schooling or active swimmers (e.g., families Atherinopsidae, Carangidae, Gerreidae, Haemulidae, Mugilidae, and Sparidae). No distributional pattern clearly linked community structure to distance from the sea and the most suggestive patterns (C, A, and D) probably include the influence of parameters, as yet unaccounted for, that act upon the fauna. Although distance from the forereef may be one of these determinant parameters, we suspect that "aloneness" of a tidepool may play an important role in concentrating, at low tide, many fish (herbivores and nonherbivores alike) of large size that were roving over the reef flat at high tide. Thus, if juvenile rovers avoid the forereef, a relatively small pool alone in a large area suitable for roving (i.e., the reef flat at high tide) would at low tide "drain" as many roving transient fish as several large pools dispersed over this same (and now unsuitable) area. Experimental substrate manipulations, such as those proposed by Griffiths (2003) and performed by Griffiths et al. (2006), Arakaki and Tokeshi (2010) and Rojas and Ojeda (2010), would permit evaluation of the importance of each factor in determining the composition and structure of pool communities.

Another factor that could influence the spatial distribution of species is intra- or interspecific resource partitioning, and either of these may cause segregation (Gibson, 1986; Faria and Almada, 1999; Zander et al., 1999; Davis, 2000; Faria and Almada, 2001; Arakaki and Tokeshi, 2010). The sympatric gobiid species *B. soporator* and *C. boleosoma* display frequent intra- and interspecific agonistic behavior. In particular, *B. soporator* feeds on *C. boleosoma* and, occasionally, cannibalizes smaller individuals (senior author, personal observ.). For both species, territoriality explains agonistic behavior between conspecific individuals. The two species share the same preference for eurythermal-euryhaline pools and interspecific interactions result from niche overlap. These interactions could theoretically result in spatial segregation, but there is no clear evidence that such a process occurs at Praia do Castelhanos. Further study is necessary to comprehend the importance of interspecific interactions in the distribution of these species.

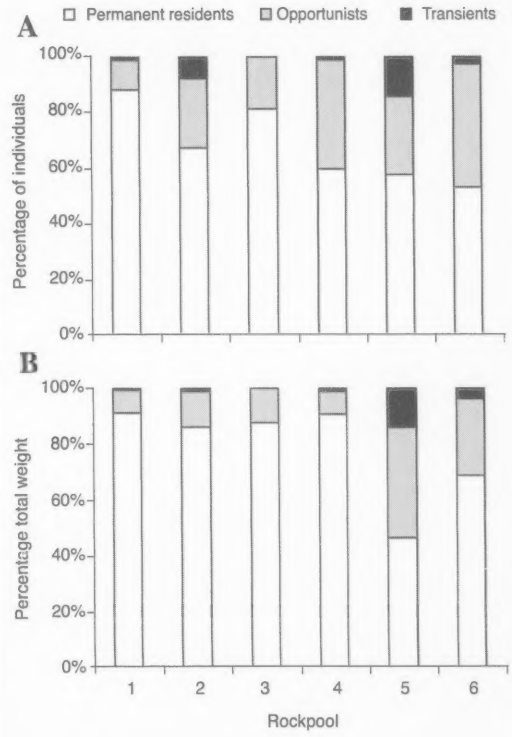

Figure 5

(**A**) Percentage of the number of individuals, and (**B**) percentage of total weight of each residency category in pools at Praia dos Castelhanos, Espírito Santo, Brazil.

Conclusions

The main factors structuring intertidal fish communities on rocky shores (e.g., isolation, height, gradient, and exposure of tide pools to waves) were held constant at Praia dos Castelhanos. Spatial distribution of fishes only partially depended upon the physicochemical setting and was apparently independent of distance of the tide pools from the sea. The structure of the fish community within each physicochemical setting principally resulted from the synergistic interaction of niche availability (that directly depends upon pool morphometry) and ecological relationships among species (e.g., competition, territoriality, predation). Mason et al. (2008) suggested that niche complementarity (i.e. niche differences between species) prevents competitive exclusion (when one species outcompetes and displaces another by making a better use of the same critical resource) and can increase ecosystem function. Further studies should focus on niche overlap within and among species for an understanding of the influence of competition in the structuring of intertidal fish communities. Moreover, we hypothesize that pool "aloneness" (the concept here includes the degree of connectivity with other pools) influences the interactions within pools at low tide by incorporating into the pool-effect the space and niches available at high tide. The use of out-of-pool space would widely vary between direct pool-to-pool passage (e.g., *B. soporator*; Aronson, 1951) and extensive roving over nonpool space (e.g., Faria and Almada, 2006). The paradigm therefore needs to shift from isolated tidepools to pools integrated into their surroundings (pools and

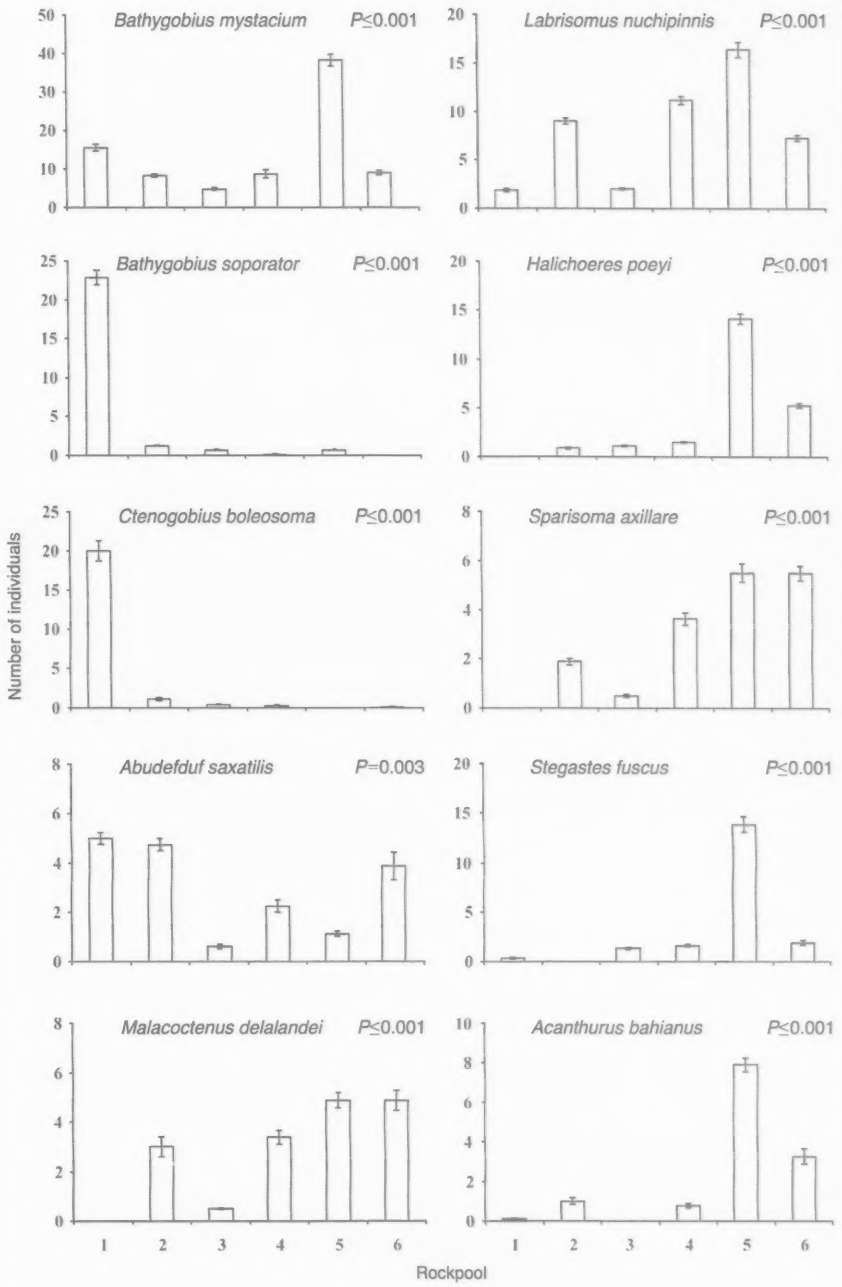

Figure 6

Mean (±1 standard error) number of individuals for the ten most abundant species in pools at Praia dos Castelhanos, Espírito Santo, Brazil. The results of Friedman tests (n=8) for differences in number of individuals among pools are inserted in the graphs.

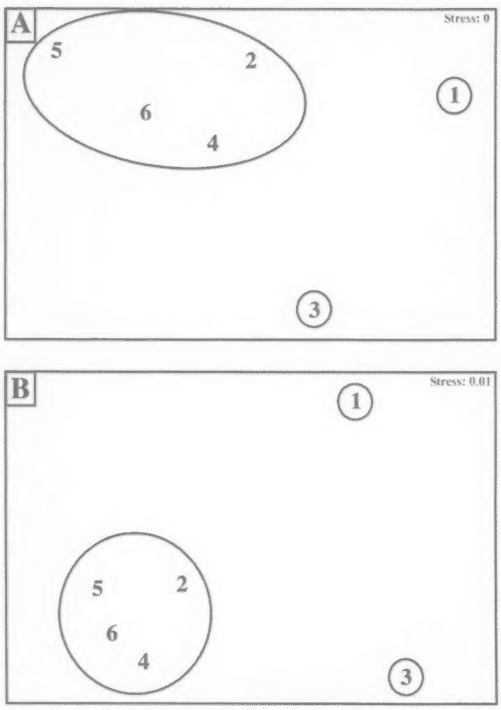

Figure 7

Nonmetric multidimensional scaling plot for a comparison of the centroids for (**A**) total abundance and (**B**) total weight for the fish community from pools at Praia dos Castelhanos, Espírito Santo, Brazil. Matrices were built by using the Bray-Curtis coefficient, and data were transformed (4^{th} root) to reduce the influence of abundant taxa. Numbers (1–6) are the numbers assigned to the tide pools (see Fig. 1).

nonpools alike) to incorporate the full complement of species' behavior for a more complete understanding of how intertidal fish species use and survive in a challenging environment.

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Literature cited

Arakaki, S., and M. Tokeshi.
2010. Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments. J. Anim. Ecol. 80:137–147. doi: 10.1111/j.1365–2656.2010.01749.x

Aronson, L. R.
1951. Orientation and jumping behavior in the gobiid fish *Bathygobius soporator*. Am. Mus. Nat. Hist. 1486:1–22.

Bennett, B. A., and C. L. Griffiths.
1984. Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. S. Afr. J. Zool. 19:97–104.

Castellanos-Galindo, G. A., A. Giraldo, and E. A. Rubio.
2005. Community structure of an assemblage of tidepool fishes on a tropical eastern Pacific rocky shore, Colombia. J. Fish. Biol. 67:392–408.

Davis, J. L. D.
2000. Spatial and seasonal patterns of habitat partitioning in a guild of southern California tidepool fishes. Mar. Ecol. Prog. Ser. 196:253–268.

Evans, D. H., J. B. Claiborne, and G. A. Kormanik.
1999. Osmoregulation, acid-base regulation and nitrogen excretion. *In* Intertidal fishes: life in two worlds (M. H. Horn, K .L. M. Martin, and M. A. Chotkowski, eds.), p. 79–92. Academic Press, San Diego, CA.

Faria, C., and V. Almada.
1999. Variation and resilience of rocky intertidal fish in western Portugal. Mar. Ecol. Prog. Ser. 184:197–203.
2001. Microhabitat segregation in three rocky intertidal fish species in Portugal: does it reflect interspecific competition? J. Fish Biol. 58:145–159.
2006. Patterns of spatial distribution and behaviour of fish on a rocky intertidal platform at high tide. Mar. Ecol. Prog. Ser. 316:155–164.

Gibson, R. N.
1972. The vertical distribution and feeding relationships of intertidal fish on the Atlantic Coast of France. J. Anim. Ecol. 41:189–207.
1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Annu. Rev. 20:363–414.
1986. Intertidal teleosts: life in a fluctuating environment. *In* The behavior of teleosts fishes (T. I. Pitcher, ed.), p. 388–407. Croom Helm, London.
1999. Methods for studying intertidal fishes. *In* Intertidal fishes: life in two worlds (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), p. 7–25. Academic Press, San Diego, CA.

Gibson, R. N., and R. M. Yoshiyama.
1999. Intertidal fishes communities. *In* Intertidal fishes: life in two worlds (M. H. Horn, K .L. M. Martin, and M. A. Chotkowski, eds.), p. 264–296. Academic Press, San Diego, CA.

Griffiths, S. P.
2003. Rockpool ichthyofaunas of temperate Australia: species composition, residency and biogeographic patterns. Estuar. Coast. Shelf Sci. 58:173–186.

Griffiths, S. P., A. R. Davis, and R. J. West.
2006. Role of habitat complexity in structuring temperate rockpool ichthyofaunas. Mar. Ecol. Prog. Ser. 313:227–239.

Grossman, G. D.
1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119(5):611–637.

Lawson, G. L., D. L. Kramer, and W. Hunte.
1999. Size-related habitat and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. Environ. Biol. Fishes 54:19–33.

Mahon, R., and S. D. Mahon.
1994. Structure and resilience of a tidepool fish assemblage at Barbados. Environ. Biol. Fishes 41:171–190.

Mason, N. W. H., C. Lanoiselée, D. Mouillot, J. B. Wilson, and C. Argillier.
2008. Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. J. Anim. Ecol. 77:661–669.

Nelson, J. S.
2006. Fishes of the world, 4th ed., 624 p. Wiley, New York.

Polivka, K. M., and M. A. Chotkowski.
1998. Recolonization of experimentally defaunated tidepools by Northeast Pacific intertidal fishes. Copeia 1998:456–462.

Raffaelli, D., and S. Hawkins.
1996. Intertidal ecology. Chapman and Hall, London.

Rojas, J. M., and F. P. Ojeda.
2010. Spatial distribution of intertidal fishes: a pattern dependent on body size and predation risk? Environ. Biol. Fishes 87:175–185.

Thompson, R. C., T. P. Crowe, and S. J. Hawkins.
2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environ. Conserv. 29(2):168–191.

Villéger, S., J. R. Miranda, D. F. Hernández, and D. Mouillot.
2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20:1512–1522.

Wilding T. A., E. J. L. Palme, and N. V. C. Polunin.
2010. Comparison of three methods for quantifying topographic complexity on rocky shores. Mar. Environ. Res. 69:143–151.

Zander C. D., J. Nieder, and K. Martin.
1999. Vertical distribution patterns. *In* Intertidal fishes: life in two worlds (M. H. Horn, K .L. M. Martin, and M. A. Chotkowski, eds.), p. 26–53. Academic Press, San Diego, CA.

Zar, J. H.
1999. Biostatistical analysis, 4th ed. Prentice Hall, New Jersey.

Regional variation in the annual feeding cycle of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska

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Abstract—Juvenile fish in temperate coastal oceans exhibit an annual cycle of feeding, and within this cycle, poor wintertime feeding can reduce body growth, condition, and perhaps survival, especially in food-poor areas. We examined the stomach contents of juvenile walleye pollock (*Theragra chalcogramma*) to explain previously observed seasonal and regional variation in juvenile body condition. Juvenile walleye pollock (1732 fish, 37–250 mm standard length) of the 2000 year class were collected from three regions in the Gulf of Alaska (Kodiak, Semidi, and Shumagin) representing an area of the continental shelf of ca. 100,000 km^2 during four seasons (August 2000 to September 2001). Mean stomach content weight (SCW, 0.72% somatic body weight) decreased with fish body length except from winter to summer 2001. Euphausiids composed 61% of SCW and were the main determinant of seasonal change in the diets of fish in the Kodiak and Semidi regions. Before and during winter, SCW and the euphausiid dietary component were highest in the Kodiak region. Bioenergetics modeling indicated a relatively high growth rate for Kodiak juveniles during winter (0.33 mm standard length/d). After winter, Shumagin juveniles had relatively high SCW and, unlike the Kodiak and Semidi juveniles, exhibited no reduction in the euphausiid dietary component. These patterns explain previous seasonal and regional differences in body condition. We hypothesize that high-quality feeding locations (and perhaps nursery areas) shift seasonally in response to the availability of euphausiids.

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In temperate and subpolar oceans, many coastal fishes exhibit an annual cycle in feeding due to seasonal changes in prey availability and composition (Wootton, 1998). The cyclical low point in feeding conditions often occurs during winter when environmental conditions can adversely affect growth and survival of juveniles and thereby constrain year-class strength (Sogard, 1997; Hurst, 2007). However, juveniles that inhabit prey-rich areas may fare better than those in prey-poor areas because of enhanced accumulations of body reserves before winter, acquisition of energy during winter, or both. Thus, prey-rich areas may support relatively high growth and survival and thereby function as important nurseries for the production of recruits (Dahlgren et al., 2006).

Walleye pollock (*Theragra chalcogramma*) is prominent in many North Pacific ecosystems as a major food web component and fishery resource (Springer, 1992). In the Gulf of Alaska (GOA), juvenile walleye pollock are one of the most abundant neritic forage fishes and are consumed by seabirds, fishes, and marine mammals (Brodeur and Bailey, 1996). Predation-related mortality of juveniles can significantly determine walleye pollock year-class strength in the GOA (Bailey, 2000). Because juveniles require food to grow, and mortality can decrease with body size (Sogard, 1997), description of the annual feeding cycle will provide a trophic context for annual cycles in growth (Brodeur and Wilson, 1996) and mortality (e.g., Hurst, 2007). Furthermore, year after year, specific regions of the GOA support juvenile walleye pollock that are larger (Wilson, 2000; Wilson et al., 2009) and in better body condition (Buchheister et al., 2006) than members of the same year class from other regions, thus raising the possibility that seasonal changes in habitat quality (e.g., food resources) vary geographically.

In the GOA, the principal habitat of juvenile walleye pollock occurs from Kodiak Island to Unimak Pass (Brodeur and Wilson, 1996) (Fig. 1). Young-of-the-year (age-0) juveniles are particularly abundant in the Semidi Bank region because of downstream advection of larvae produced by the large spawning aggregation that forms during early spring in Shelikof Strait (Hinckley et al., 1991). During winter, growth of age-0 juveniles decreases to a negligible rate when epibenthic foraging supplements the acquisition of pelagic prey (Brodeur and Wilson, 1996). In addition,

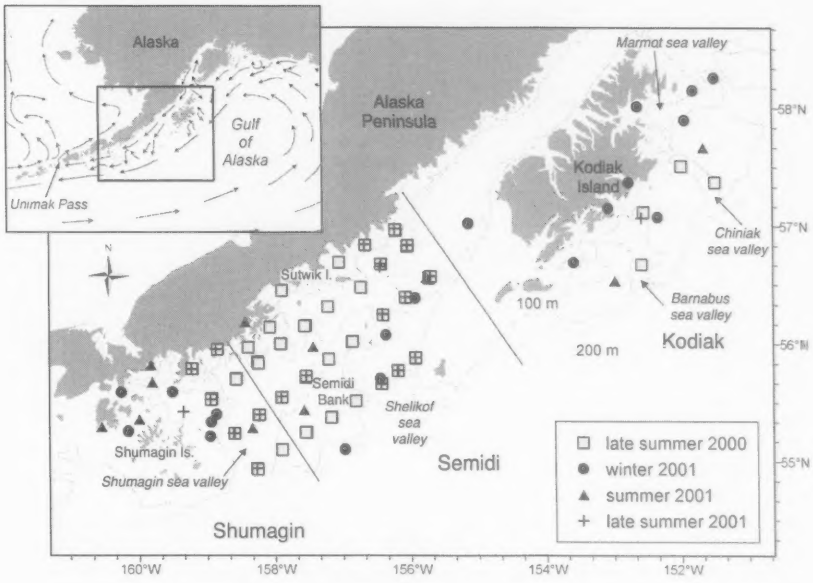

Figure 1

Sites where juvenile walleye pollock (*Theragra chalcogramma*) were collected with trawl nets in the Gulf of Alaska from August 2000 to September 2001. Delineation of season and geographic region follow Buchheister et al. (2006) (see Table 1 for specific sampling dates). Arrows in inset represent the predominant currents in Alaskan waters (Reed and Schumacher, 1986).

a persistent along-shore shift in body length of age-0 juveniles occurs at about Sutwik Island and relatively large juveniles are found northeastward in the Kodiak Island region (Wilson, 2000). In addition to larger body lengths, these juveniles also have greater length-specific weights and are more energy dense than fish from other regions, particularly in late summer and winter (Buchheister et al. 2006). The underlying cause remains unproven but likely involves some aspect of feeding ecology. For example, juveniles collected near Kodiak Island during late summer had a euphausiid-rich diet (Merati and Brodeur, 1996; Wilson et al., 2005; Wilson et al., 2009) and faster growth (Bailey et al., 1996) than individuals collected in the Semidi Bank vicinity. There is currently insufficient evidence in the literature to evaluate the role of food habits in determining regional and cyclical variation in growth, body condition, and perhaps survival of juvenile walleye pollock in the western GOA.

Our objective was to examine the food habits of juvenile walleye pollock for evidence of an annual cycle and to elucidate how these food habits may vary regionally in relation to previously observed geographic variation in juvenile body condition and growth rate. The focus on one year class simply reflects sample availability. Samples of the 2000 year class were available from directed sampling during late summer 2000 (age-0 juveniles) and during late summer 2001 (age-1 juveniles). An additional set of samples was available from opportunistic sampling. Examining fish from these sample sets enabled us to provide new insight and formulate hypotheses about annual periodicity and regional variation in the food habits of juvenile walleye pollock. Previously, all or a subset of these same samples were used to examine body condition (Buchheister et al., 2006) and growth rates of juvenile walleye pollock (Mazur et al., 2007; Wilson et al., 2011). We conducted a modeling exercise to integrate these previous findings with our observations on food habits and explore the implication of these results on juvenile walleye pollock growth rate.

Materials and methods

Sample collection

Juvenile walleye pollock were collected from 124 trawl catches in the western GOA during August 2000 to September 2001 during nine research cruises conducted by the National Marine Fisheries Service (NMFS). Samples were grouped according to collection location and date according to the method of Buchheister et al. (2006). There were three geographic regions (Kodiak, Semidi, and Shumagin) and four seasons (late summer 2000 [LSum00], winter 2001 [Win01], summer 2001 [Sum01], and late summer 2001 [LSum01]) (Table 1, Fig. 1). The geographic divisions within the experimental study area somewhat arbitrarily distinguished alongshore regions

Table 1

Juvenile walleye pollock (*Theragra chalcogramma*) (1732 fish) were collected in 124 trawl catches (i.e., samples) from three regions of the western Gulf of Alaska during four seasons from August 2000 to September 2001. Fish size is indicated by mean standard length (standard error) and range (minimum–maximum).

Region	Season	Collection date	No. of samples	No. of fish	Standard length (mm)	
					Mean (SE)	Range
Kodiak	Late summer 2000	15–19 Aug 2000	4	63	71 (0.7)	57–88
	Winter 2001	1 Feb–21 Mar 2001	9	78	122 (1.6)	95–158
	Summer 2001	26 Jun–8 Jul 2001	2	20	165 (2.7)	144–182
	Late summer 2001	3 Sep 2001	1	7	200 (2.3)	192–207
Semidi	Late summer 2000	8–19 Sep 2000	45	784	71 (0.4)	37–109
	Winter 2001	2 Feb–23 Mar 2001	4	38	107 (2.1)	83–127
	Summer 2001	9–15 Jun 2001	4	40	118 (1.9)	96–145
	Late summer 2001	8–18 Sep 2001	20	161	198 (2.1)	136–250
Shumagin	Late summer 2000	4–7 Sep 2000	16	374	60 (0.4)	43–86
	Winter 2001	14 Feb–9 Mar 2001	6	58	103 (1.8)	82–153
	Summer 2001	2–7 Jun 2001	5	46	118 (1.7)	95–149
	Late summer 2001	4–7 Sep 2001	8	63	173 (3.3)	127–232

of the shelf according to prominent bathymetric features (Fig. 1) and covered the area alongshore where there is a shift in body length of age-0 walleye pollock (Wilson, 2000). The use of this scheme facilitated integration of our results with those of Buchheister et al. (2006) in our modeling exercise.

Two of the nine cruises were regularly scheduled by NMFS to study juvenile walleye pollock. Samples were collected at predetermined sites between Shelikof Strait and the Shumagin Islands during 3–19 September 2000 and 3–18 September 2001. Samples were collected without regard to time of day with a Stauffer (anchovy) midwater trawl (Wilson et al., 1996). The trawl was equipped with a 3-mm mesh codend liner, and it was fished over double-oblique tows to a depth of 200 m or to 10 m off bottom, whichever was shallowest. These two cruises produced 90 samples. Originally, the data from these samples were obtained for a multiyear study of food habits of walleye pollock (Wilson et al., 2009).

The remaining seven cruises provided all the samples from Win01 and Sum01, and most of the samples from the Kodiak region. Collections of juvenile walleye pollock on these cruises were ancillary to primary cruise objectives (i.e., opportunistic); consequently, we had little control over sampling effort, date, collection site location, and method of sampling (e.g., gear, time of day). On four of these cruises, samples were collected without regard to time of day with midwater and bottom trawls equipped with 32-mm mesh codend liners. On the remaining three cruises, samples were collected during daylight with a poly-nor'eastern bottom trawl equipped with a 32-mm mesh codend liner. These seven cruises produced 34 samples. On all nine cruises, walleye pollock were sorted from the catch and frozen for subsequent examination of their stomach contents in the laboratory.

Stomach content analysis

Fish were selected from thawed samples by standard length (SL) to narrow the focus of our study to members of the 2000 year class. Age-0 individuals were easily identified from historical distinctions in size that separated them from the next older cohort (Brodeur and Wilson, 1996). Age-0 individuals were obtained from samples collected in LSum00 and Win01. Age-1 individuals were obtained from samples collected later in Win01, and in Sum01 and LSum01. The upper SL limit of age-1 fish was estimated from NMFS length-at-age data according to the method of Buchheister et al. (2006).

Fish food habits were characterized by total stomach content weight (SCW) and taxonomic composition (by prey weight and number). Fish were thawed in seawater, measured to the nearest mm SL, blotted dry, and weighed to the nearest 1 mg (as in Wilson et al. [2009]). Stomachs were excised and preserved in 10% formalin. Later, stomachs were dissected and the contents were blotted dry, weighed to the nearest 0.01 mg, and sorted by taxonomic group. Although most copepods were calanoids, some harpacticoids were detected and quantified separately. The calanoids, hereafter referred to as copepods, were further divided by size: 1) small copepods (<2 mm prosomal length [PL]); and 2) large copepods (>2 mm PL). Euphausiids were divided into the following developmental stages: 1) furciliae (≤5 mm length, Siegel [2000]); and 2) juveniles and adults. For each taxonomic group, the total weight and total count of largely intact (ca. <50% digested) individuals were used to estimate mean weight per individual prey item. Items in each group were enumerated and weighed collectively to the nearest 0.01 mg after being blotted dry.

Data analysis

Stomach content data were used to estimate food consumption and diet composition. The amount of food consumed was assessed by using SCW normalized to somatic body weight (whole-body wet weight less stomach content weight) and expressed as percent somatic body weight (%BW). Diet composition was quantified by using prey counts or weights summed across fish and then expressing them as a percentage of total prey count or weight (%No., %W, respectively). We also computed the frequency of occurrence of a particular prey type as the percentage of all stomachs containing that particular prey type (%FO). The cumulative number of prey types detected was examined in relation to the number of fish examined, as in Ferry and Cailliet (1996). We did not incorporate estimates of fish catch in our computations (e.g., cluster sampling estimator [Buckel et al., 1999]) because of uncertainty about how to standardize sampling effort among the different gears, sampling objectives, and methods used during the various cruises.

We conducted a modeling exercise to integrate our observations on feeding with previous findings on body condition (Buchheister et al., 2006) and prey energy density (Mazur et al., 2007) to explore the implications for juvenile walleye pollock growth. The exercise consisted of first estimating daily ration (DR), and then inputting it and other empirical data into a bioenergetics model to output fish growth rate. Daily ration was estimated empirically with a simple evacuation rate model (Elliott and Persson, 1978):

$$C = 24 \cdot E \cdot \bar{S}, \quad (1)$$

where C = daily food consumption (%BW/d);
24 = the number of hours in a day;
E = the instantaneous rate of evacuation (%BW/h); and
$\bar{S}$ = average SCW over the course of the day.

We used E=0.28 %BW/h (Merati and Brodeur, 1996). $\bar{S}$ was computed as the average of mean SCW for each 3-h time bin (e.g., 0–3, >3–6, >6–9 h) (Elliott and Persson, 1978). All SCWs were arcsine transformed so that the errors approximated a normal distribution.

Growth rate was estimated with an age-0 walleye pollock bioenergetics model (Ciannelli et al., 1998). Model inputs were fish body weight (g), diet (%W), DR (%BW), predator energy density (J/g, Buchheister et al., 2006), taxon-specific prey energy densities (J/g, Mazur et al., 2007), and water temperature (°C). Fresh fish body weight was estimated from mean whole wet weight of thawed fish by using fresh-frozen weight relationships (Buchheister and Wilson, 2005). Predator energy density was estimated by using fish body weight-energy density relationships (A. Buchheister, unpubl. data, but see Buchheister et al., 2006). Water temperature at a depth of 40 m was measured with a calibrated SBE-19 or SBE-39 temperature profiler (Sea-Bird Electronics, Bellevue, WA), or a microbathythermograph (Richard Brancker Research, Ltd., Ontario, Canada) and averaged across sites where fish were collected. Model output growth rates were based on estimates of excess daily consumption of prey in grams of food per gram of body weight per day (g/g/d) after budgeting for egestion, excretion, respiration, and specific dynamic activity. We used the length-weight relationships from Buchheister et al. (2006) to convert growth rate units to mm SL/d for direct comparison with otolith-based growth rates.

Results

Most of the 1732 juvenile walleye pollock examined were from the Semidi and Shumagin regions during LSum00 (Table 1) when samples were collected with midwater trawl nets. The use of different survey gear (i.e., midwater or bottom trawl nets) among research cruises did not appear to influence fish size or stomach content weight. When compared by season and region, neither mean SL (ANOVA, P=0.101), nor mean stomach content weight (ANOVA, P=0.102), differed by survey gear. The bulk of the stomach contents (61%) was composed of juvenile and adult euphausiids, which also did not significantly vary by survey gear (ANOVA, P=0.426).

Stomach content weight

Overall, SCW averaged 0.72% BW, but season-to-season fluctuations were evident within each region. In all regions, mean SCW decreased from LSum00 to Win01 and then increased into Sum01 before continuing to decline (Fig. 2). The Semidi region was associated with low mean SCW (0.14–0.82% BW) compared to all other regions except Kodiak during LSum01 (0.10% BW), which was represented by only seven fish. The Kodiak region had the highest mean SCW during LSum00 (1.40% BW) and during Win01 (0.56% BW). Later, the Shumagin region had the highest mean SCW during Sum01 (0.76% BW) and LSum01 (0.49% BW), but we acknowledge low confidence in the Shumagin-Kodiak comparison because of the low number of fish available from the Kodiak region. Thus, the region with the highest mean SCW appeared to have shifted from Kodiak to Shumagin after Win01.

Diet

The cumulative number of identifiable prey types encountered in juvenile walleye pollock reached an asymptote at 16 after the contents of about 60 stomachs were examined (Fig. 3). Overall, 19 categories of items were represented in juvenile walleye pollock stomachs, but we did not consider two of these categories to be part of the diet (hard items [e.g., sand] and parasites), and one category consisted of unidentifiable items (Table 2). As the number of stomachs examined decreased below 60, the cumulative number of prey types dropped sharply, causing a negative bias on diet breadth. The smallest sample

sizes were from opportunistic sampling, which occurred during Win01, Sum01, and in the Kodiak region.

Frequently encountered prey types tended to have low individual weights, except for juvenile and adult euphausiids (Table 2). Copepods, larvaceans, and pteropods (Thecosomata) each occurred in >20% of the stomachs and had mean individual prey weights <0.8 mg. Fish (Osteichthyes) were relatively uncommon (4.3% FO) and had the highest mean individual weight (626 mg). In contrast, euphausiid juveniles and adults occurred in half the stomachs and each individual weighed on average 19.9 mg.

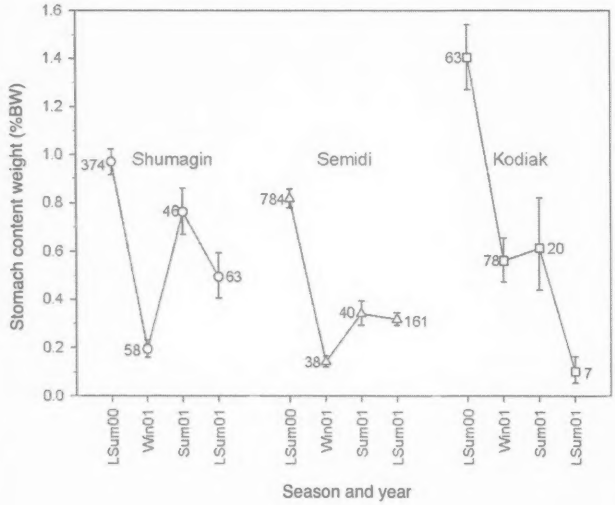

Figure 2

Mean stomach content weight (% body weight [BW] ±1 standard error) of juvenile walleye pollock (*Theragra chalcogramma*) collected with trawl nets in three regions (Shumagin, Semidi, and Kodiak) of the western Gulf of Alaska during late summer 2000 (Lsum00), winter 2001 (Win01), summer 2001 (Sum01), and late summer 2001 (Lsum01). The numbers of fish examined are indicated next to each point.

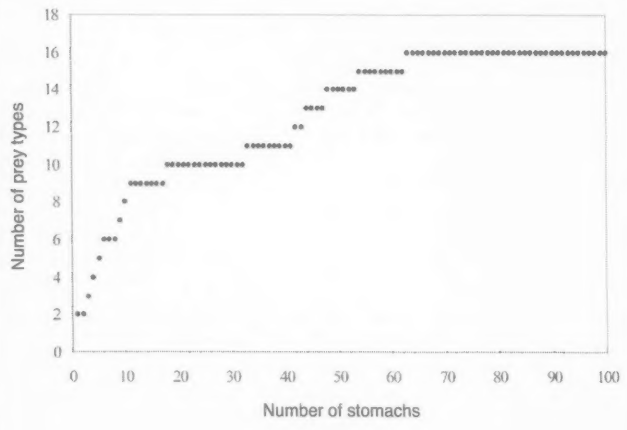

Figure 3

Number of prey types (•) (identified in stomachs of juvenile walleye pollock (*Theragra chalcogramma*) collected in trawl nets in three regions of the western Gulf of Alaska during four seasons (August 2000–September 2001). The *x*-axis is truncated at 100 stomachs.

The percentage of small-size prey abundance in juvenile walleye pollock diets declined with seasonal progression (Fig. 4A) and with increased predator length (Fig. 4C) and was primarily due to declining percentages of small copepods and larvaceans and increasing percentages of large copepods and euphausiids. For euphausiids, the proportion of furciliae peaked in Sum01, whereas the proportion of juvenile and adult euphausiids peaked later, during LSum01.

Seasonal change in diet composition by weight was most influenced by the proportion of juvenile and adult euphausiids (Fig. 4B), which overall composed 61% of the SCW. In the Shumagin region, the proportional weight of euphausiids increased from 36% in LSum00 to 64% in Sum01; subsequently, in LSum01, 51% of the stomach contents were euphausiid juveniles and adults and 40% were fish. Greater seasonality was observed in the Semidi and Kodiak fish diets. In the Semidi region, euphausiids were more important during late summer (>60%) than during Win01 and Sum01 (<20%) when diets were dominated by large copepods. In the Kodiak region, euphausiids represented >60% of the diet in all seasons except during Sum01 when most (84%) of the diet bulk was fish and other epibenthos (mostly cumaceans). The low number of Kodiak fish examined during Sum01 (20 fish) and LSum01 (7 fish) reduced confidence in the respective diet compositions. Thus, seasonality in diet composition was mostly attributable to euphausiids and was less evident in the Shumagin region than in the Semidi and perhaps Kodiak regions.

Growth rate

Growth rate estimates ranged from −0.38 mm SL/d during Win01 to 0.56 mm SL/d during LSum01, but were not estimated for all season-region combinations (Table 3). For six season-region combinations, coverage of diel periodicity in feeding (e.g., Merati and Brodeur, 1996) was deemed inadequate because <5 of the eight 3-h time bins that compose the diel feeding cycle were represented. Consequently, growth rates were

Table 2

Prey groups recovered from the stomach contents of juvenile walleye pollock (*Theragra chalcogramma*) collected during August 2000 to September 2001 by trawling in the western Gulf of Alaska. Diet composition is characterized by percent frequency of occurrence (%FO), percent of total prey count (%No), and percent of total prey weight (%W). Weight (mg) per individual prey item (W per item) indicates relative prey size.

Prey group	%FO	%No	%W	W per item[1]
Amphipoda, epibenthic	6.7	0.47	0.86	4.57
Amphipoda, pelagic	8.8	0.43	0.42	2.37
Cirripedia larvae	5.7	1.72	0.07	0.08
Copepoda, <2 mm PL	56.4	44.59	2.30	0.11
Copepoda, >2 mm PL	42.4	14.04	5.84	0.76
Chaetognatha	12.5	0.55	1.93	9.54
Euphausiacea furciliae	10.0	1.85	0.58	0.25
Euphausiacea juveniles and adults	49.6	7.53	61.32	19.91
Larvacea	32.7	17.24	0.96	0.12
Mysidacea	0.9	0.03	0.24	14.52
Natantia	2.1	0.06	1.13	65.09
Osteichthyes	4.3	0.10	14.35	626.48
Reptantia	20.4	1.04	2.24	5.77
Thecosomata	21.3	6.94	0.85	0.16
miscellaneous prey (e.g., Ostracoda)	3.7	0.31	0.05	0.12
hard items (e.g., sand)	0.9	0.00	0.18	2.70
other epibenthic prey (e.g., Cumacea, harpacticoids)	5.1	2.06	3.35	1.92
parasites (e.g., Nematoda)	10.4	0.33	0.68	3.62
unidentified prey	45.4	0.71	2.65	0.15
Groups combined	100	100	100	2.72

[1] Per item weight (W/No.) was computed with only items that were <50% digested

estimated for only the six remaining season-region combinations.

Absolute growth rate (mm SL/d) generally increased with seasonal progression, except during Win01 when growth in the Shumagin region was negative. Compared to the growth of Kodiak fish, the negative growth of Shumagin fish was associated with relatively small-fish body weight, low daily ration, and an energy-poor diet. In terms of specific growth rate, the negative wintertime growth equates to a daily loss of 1% BW for Shumagin juveniles; in contrast, the positive wintertime growth of the Kodiak juveniles equates to a daily gain of 1% BW. It therefore appears that the higher daily ration and energy-rich diet observed among juveniles in the Kodiak region during Win01 resulted in a relatively high season-specific growth rate.

Discussion

Our results show that members of the largest population of juvenile walleye pollock in the GOA exhibit seasonal fluctuations in stomach content weight similar to those of other cold-water fishes (Wootton, 1998). Because these were growing juveniles, the feeding cycle was superimposed on marked increases in fish body size. Body size is an important consideration because increases in body size generally correspond with decreases in the specific weight of stomach contents (Wootton, 1998). Thus, the late summer-to-winter and the summer-to-late summer declines in %BW can be at least partly explained by increasing fish length. However, a length effect does not explain the winter-to-summer rebound in stomach content weight, which might alternatively be explained by a postwinter rebound from relatively poor wintertime feeding conditions. We acknowledge that the Kodiak region in particular was represented by few fish, which increases uncertainty in our observations, but the seasonal pattern was similar among regions and was consistent with a postwinter recovery in body condition (Buchheister et al., 2006) and acceleration in growth rate (Wilson et al., in press). The increase in water temperature from winter to summer may have stimulated feeding by increasing gastric evacuation and systemic demand (Wootton, 1998). Another contributing factor might have been prey availability. Zooplankton population density in the GOA increases during spring owing to an early summer peak in copepod abundance before declining from summer to winter (Coyle and Pinchuk, 2003). Prey availability was thought to influence positively stomach content weights of walleye pollock in the Bering Sea (Dwyer et al., 1987).

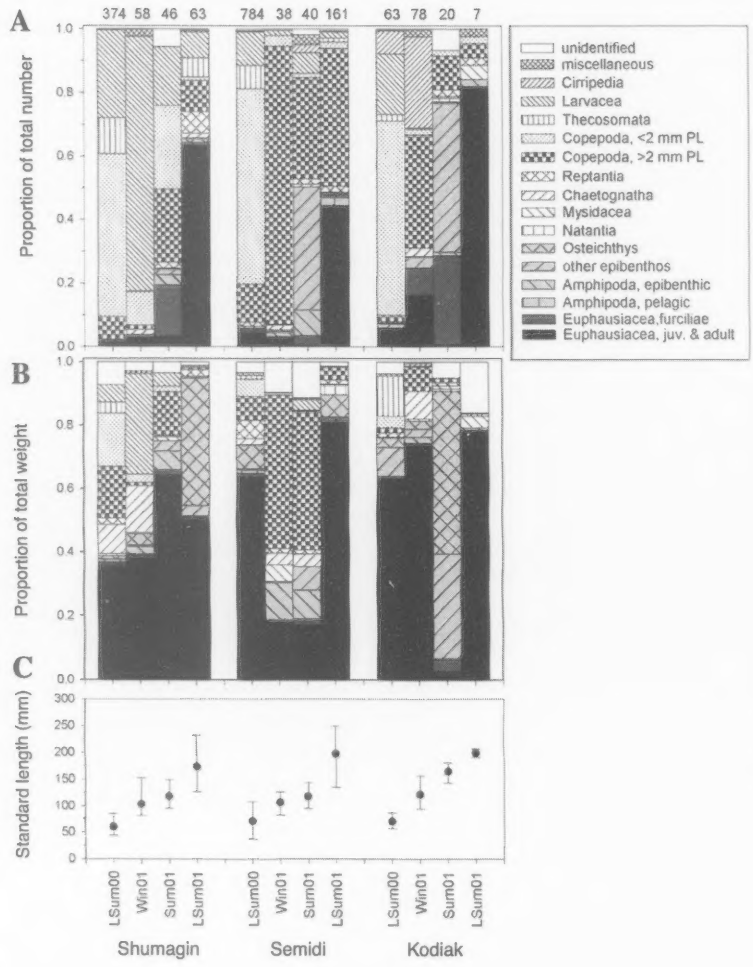

Figure 4

Diet composition for juvenile walleye pollock (*Theragra chalcogramma*) collected in trawl nets in three regions of the western Gulf of Alaska during four seasons (August 2000–September 2001). Diet is based on taxonomic composition of stomach contents by prey count (**A**) and weight (**B**). Predator size is indicated by the mean and range of standard length (**C**). Numbers of fish examined are shown along the top of graph A. PL=prosomal length.

Stomach content weight and diet were not strictly independent because euphausiids were a principal dietary component. A similar association was inferred off Japan when a postwinter rebound in juvenile walleye pollock stomach fullness was thought to reflect seasonal increase of euphausiid abundance (Yamamura et al., 2002). Euphausiids are a preferred prey item (Wilson et al., 2006) and the large ones especially are a beneficial dietary addition because their caloric density is higher than that of most other prey (Mazur et al., 2007). However, the consumption of large euphausiids may be constrained by fish mouth gape width (Brodeur, 1998). The constraint relates to body size (Wilson et al., 2009). Given the negligible overwinter growth, from age-0 to age-1 (Brodeur and Wilson, 1996), we hypothesize that poor wintertime food habits resulted at least partly from juvenile walleye pollock being too small to consume all sizes of euphausiids.

The annual cycle of euphausiids in juvenile walleye pollock diet likely reflects the predator-prey size relationship superimposed on annual cycles of fish growth and euphausiid production. In the GOA, euphausiids

are spawned during spring (Pinchuk et al., 2008) and then develop and grow during the subsequent summer (Pinchuk and Hopcroft, 2007). This can explain why the peak proportion of furciliae in fish stomachs preceded that of juvenile and adult euphausiids. Euphausiid population density appears to peak during autumn (Coyle and Pinchuk, 2005) or winter (Cooney, 1986) owing perhaps to prespawning aggregation behavior and sampling bias (e.g., Siegel, 2000). We contend that some fraction of these euphausiids were too big to be available as prey of late age-0 and early age-1 walleye pollock. Any starvation-related shrinkage in euphausiid body size (Pinchuk and Hopcroft, 2007) might therefore benefit juvenile walleye pollock. Sometime between the period when walleye pollock growth resumes in early spring (Wilson et al., in press) and the period when they consume large euphausiids in late summer (Wilson et al., 2009), yearling walleye pollock gain the ability to consume all sizes of the euphausiids within their foraging ambit. Because juvenile walleye pollock and euphausiid size compositions vary geographically (e.g., Wilson et al., 2009), we predict that regional variation occurs in the timing when juveniles gain full access to all sizes of euphausiids, which are a principal determinant of food-related habitat quality.

Superior feeding conditions before and during winter in the Kodiak region can explain why resident juveniles were bigger and in better body condition than other juveniles (Buchheister et al., 2006). Superior feeding conditions were indicated by a euphausiid-rich diet and fuller stomachs. Euphausiid-rich diets may simply reflect the advantage of a body size that enabled the consumption of large euphausiids. However, recent research during late summer indicates that euphausiid populations in the Kodiak region can be substantially denser than in the Shumagin and Semidi regions (senior author, unpubl. data) and perhaps reflect different oceanographic characteristics. The Kodiak region is characterized by onshore flow into sea valleys, which were associated with euphausiid concentrations (Logerwell et al., 2010). In contrast, much of the shelf area in the Shumagin and Semidi regions is occupied by Semidi Bank, which causes offshore flow (Schumacher and Reed, 1986). Few euphausiids occur inshore of and over Semidi Bank, although concentrations are found over the adjacent continental slope and sea valleys (Wilson, 2009). Euphausiids may also experience less grazing pressure in the Kodiak region than in the Shumagin and Semidi regions where juvenile walleye pollock can be more abundant (senior author, unpubl. data).

During summer 2001, the best food-related habitat quality for juvenile walleye pollock appeared to have shifted to the Shumagin region. The Shumagin juveniles experienced the strongest postwinter rebound in stomach fullness and no decline in the dietary proportion of euphausiids. This shift in habitat may reflect the relatively high abundance of small-size euphausiids observed later in the region (Wilson et al., 2009). In contrast, Semidi and Kodiak juveniles exhibited a relatively weak postwinter rebound in stomach fullness and relatively low euphausiid dietary proportions. The high proportion of epibenthic animals (e.g., cumaceans) among Kodiak fish during summer 2001 may be indicative of supplemental feeding during times of pelagic prey scarcity (Brodeur and Wilson, 1996). The better habitat quality in the Shumagin region may have been transitory as the diets of juveniles in the Semidi and Kodiak areas again became relatively euphausiid rich during late summer 2001, although the Shumagin mean SCW stayed relatively high. We acknowledge that our interpretation of apparent differences between Shumagin and Kodiak is tenuous given the paucity of Kodiak fish examined—a paucity that can bias dietary breadth (Ferry and Cailliet, 1996) and reduce estimate precision, but our interpretation is consistent with season and region differences in body condition.

Additional support of a postwinter shift in the region of most-favorable feeding habitat is provided by regional differences in whole-body energy density. In concert with their relatively strong postwinter rebound in stomach content weight, Shumagin fish exhibited a stronger rebound in whole-body energy density than Semidi and Kodiak juveniles, and the Shumagin juveniles had high energy densities during summer 2001 (Buchheister et al., 2006). We therefore hypothesize that the area most favorable for juvenile walleye pollock feeding is determined by euphausiid availability and shifts from the Kodiak region during winter to the Shumagin region during summer. Whether this change extends to seasonal shifts in walleye pollock nursery location, as distinguished from less productive juvenile habitat (Dahlgren et al., 2006), depends on the impact that the variation in food habits has on growth and survival.

In the field context of the present study, juvenile walleye pollock food habits and associated body condition have direct implications for growth rate. The relevance of food to growth was underscored by the similarity of our growth estimates from food-based modeling with those from independent otolith-based studies. Otolith growth of age-0 walleye pollock 5 days before capture in late summer 2000 indicated body growth rates of 0.03 to 0.19 g/d (Mazur et al., 2007), which encompass our estimates of 0.03 and 0.04 g/d (see Table 3, multiply the specific growth rate by body weight). During 2001, the peak growth rate of yearling walleye pollock estimated from growth increments in otoliths was 0.59 mm SL/d (Wilson et al., in press), which was slightly above our late summer 2001 estimates of 0.39 and 0.56 mm SL/d. We found no estimates of growth rate during winter, but the average of our two new wintertime estimates (–0.03 mm SL/d) is consistent with the negligible change in body length of juveniles throughout the western GOA (Brodeur and Wilson, 1996). The difference between our winter estimates reflects the difference in dietary proportion of euphausiids associated with differences in stomach content weight and diet energy density. We speculate that similar region-specific dietary differences explain the previously observed faster growth (Bailey et al., 1996) and larger body length

Table 3

Growth rate for juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska by season and region (see Fig. 1, Table 1) was estimated with a bioenergetics model. Model inputs included mean water temperature at 40-m depth, predator body weight, predator energy density, and daily food ration. Daily ration (%BW/d) was estimated with a simple evacuation model (see text). Diet energy density and specific growth rate (grams of growth per gram of body weight per day, [g/g/d]) are included. LSum00=late summer 2000, Win01=winter 2001, and LSum01=late summer 2001.

				Energy density (J/g)			Growth rate	
Season	Region	Temp (°C)	Body wt (g)	Predator	Diet	Daily ration	mm SL/d	g/g/d
LSum00	Semidi	9.0	3.6	3999	5094	4.99	0.26	0.011
LSum00	Shumagin	8.3	2.0	3441	4070	6.62	0.27	0.013
Win01	Kodiak	5.0	15.2	4284	5261	3.46	0.33	0.008
Win01	Shumagin	4.5	9.3	4187	3530	1.30	−0.38	−0.011
LSum01	Semidi	9.8	81.4	4782	5578	2.43	0.39	0.006
LSum01	Shumagin	9.3	55.0	4576	4725	3.45	0.56	0.010

(Wilson, 2000) of age-0 juveniles in the Kodiak region during late summer. Fish body size and water temperature are other relevant factors because they affect respiration, which in the bioenergetics model was the largest use of input energy. Respiration decreases with fish size, but increases with water temperature. Thus, the wintertime size-related reduction in respiration of Kodiak fish allowed more energy for growth than that for Shumagin fish although water in the Shumagin region was 0.5° C cooler. In addition to physiological conditions, body size directly affects the acquisition of large euphausiids (Wilson et al., 2009) and consequent energy input (Mazur et al., 2007). For summer 2001 and late summer 2001, too few samples were available to estimate the growth rates of Kodiak yearlings for comparison with the Shumagin region and therefore we were unable to explore seasonal shifts in the region of most-favorable growth. Nevertheless, the direct implication of seasonal and regional variation in food habits on growth rate leads us to speculate that the region most favoring rapid growth of juvenile walleye pollock varies with year in response to ecological determinants of euphausiid availability and oceanographic effects on local euphausiid abundance.

Opportunistic sampling enabled us to obtain the sample set necessary to formulate hypotheses, but rigorous control over sampling effort and site location was lacking. This was least a concern during winter when sampling effort was relatively high and most sites were located in close proximity to sea valleys where yearlings likely concentrate (e.g., Hollowed et al., 2007; Wilson, 2009). However, the number of stomachs available during winter from the Semidi region was <60; therefore the apparent number of prey types consumed (i.e., dietary breadth) was probably biased low (Ferry and Cailliet, 1996). Similarly insufficient stomach numbers were available in each region sampled during summer 2001, but the negative bias was probably most extreme for Kodiak during summer and late summer 2001 when only 20 and 7 fish were examined, respectively. It was encouraging, however, that the late summer 2001 resurgence in the dietary proportion of euphausiids among Kodiak fish was mirrored in the diet of Semidi fish, which was represented by ample stomachs. Site location in the Kodiak region during summer and late summer (2000 and 2001) was generally farther offshore than in winter. Therefore, the available samples did not represent the nearshore where juvenile walleye pollock population density can be high (Wilson et al., 2005). Previously, at least for age-0 juveniles, no significant difference was found between nearshore and shelf sites regarding stomach content weight, and dietary differences were attributed to nearshore prey (e.g., crab larvae) rather than euphausiids (Wilson et al., 2005), which in the present study were primarily responsible for diet variation. Another problem with using opportunistic sampling was the variety of cruise objectives and collection methods (e.g., gear), which created uncertainty about how to quantify the population fraction represented by each sample. Clearly, there are many drawbacks to using opportunistically collected samples; however, those samples provided the empirical information necessary to formulate our hypotheses.

Conclusions

In summary, an annual cycle in juvenile walleye pollock food habits was primarily evident as a postwinter rebound in stomach content weight that was not explained by a body-size effect. We hypothesize that seasonal changes in stomach content weight were driven by the combined effects of juvenile growth, predator-prey size constraints, and the cycle of euphausiid abundance and growth. Further, we hypothesize that the most-favorable feeding area cycles annually from the Kodiak region during winter to the Shumagin region during summer in response to euphausiid availability. The similarity in growth rate between food-based model output and independent otolith-based estimates imply that the

observed seasonal and regional variation in food habits and body condition directly affect juvenile walleye pollock growth rates. Given that food habits, body condition, and growth rate are relevant to the survival of juveniles, the location of walleye pollock nurseries, as opposed to less productive juvenile habitat (Dahlgren et al., 2006), may vary with annual periodicity.

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Literature cited

Bailey, K. M.
2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar. Ecol. Prog. Ser. 198:215–224.

Bailey, K. M., A. L. Brown, M. M. Yoklavich, and K. L. Mier.
1996. Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91. Fish. Oceanogr. 5(suppl. 1):137–147.

Brodeur, R. D.
1998. Prey selection by age-0 walleye pollock, *Theragra chalcogramma*, in nearshore waters of the Gulf of Alaska. Environ. Biol. Fishes 51:175–186.

Brodeur, R. D., and K. M. Bailey.
1996. Predation on the early life stages of marine fish: A case study on walleye pollock in the Gulf of Alaska. *In* Survival strategies in early life stages of marine resources; proceedings of an international workshop; Yokohama, Japan, 11–14 October 1994 (Y. Watanabe, Y. Yamashita, and Y. Oozeki, eds.), p. 245–259. A.A. Balkema, Rotterdam, Netherlands.

Brodeur, R. D., and M. T. Wilson.
1996. A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. Fish. Oceanogr. 5 (suppl. 1):148–166.

Buchheister, A., and M. T. Wilson.
2005. Shrinkage correction and length conversion equations for *Theragra chalcogramma, Mallotus villosus* and *Thaleichthys pacificus*. J. Fish. Biol. 67:541–548.

Buchheister, A., M. T. Wilson, R. J. Foy, and D. A. Beauchamp.
2006. Seasonal and geographic variation in condition of juvenile walleye pollock in the western Gulf of Alaska. Trans. Am. Fish. Soc. 135:897–907.

Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown.
1999. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-depended loss of juvenile striped bass (*Morone saxatilis*). Can. J. Fish. Aquat. Sci. 56:275–287.

Ciannelli, L., R. D. Brodeur, and T. W. Buckley.
1998. Development and application of a bioenergetics model for juvenile walleye pollock. J. Fish Biol. 52:879–898.

Cooney, R. T.
1986. Zooplankton. *In* The Gulf of Alaska physical environment and biological resources (D. W. Hood and S. T. Zimmerman, eds.), p. 285–303. OCS Study MMS86-0095. Minerals Management Service, Springfield, VA.

Coyle, K. O., and A. I. Pinchuk.
2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish. Oceanogr. 12:327–338.
2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep-Sea Res., pt. II, Top. Stud. Oceanogr. 52:217–245.

Dahlgren, C. P., G. T. Kellison, A. J. Adams, B. M. Gillanders, M. S. Kendall, C. A. Layman, J. A. Ley, I. Nagelkerken, and J. E. Serafy.
2006. Marine nurseries and effective juvenile habitats: concepts and applications. Mar. Ecol. Prog. Ser. 312:291–295.

Dwyer, D. A., K. M. Bailey, and P. A. Livingston.
1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci. 44:1972–1984.

Elliott, J. M., and L. Persson.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

Ferry, L. A., and G. M. Cailliet.
1996. Sample size and data analysis: Are we characterizing and comparing diet properly? *In* Feeding ecology and nutrition in fish: proceedings of the symposium on the feeding ecology and nutrition in fish; international congress on the biology of gishes, July 14–18, 1996 (D. MacKinlay and K. Shearer, eds.), p. 71–80. Am. Fish. Soc., San Francisco, CA.

Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno.
1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 48:91–98.

Hollowed, A. B., C. D. Wilson, P. J. Stabeno, and S. A. Salo.
2007. Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). Fish. Oceanogr. 16:142–154.

Hurst, T.
2007. Causes and consequences of winter mortality in fishes. J. Fish Biol. 71:315–345.

Logerwell, E. A., J. Duffy-Anderson, M. Wilson, and D. McKelvey.
2010. The influence of pelagic habitat selection and inter-

specific competition on productivity of juvenile walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) in the Gulf of Alaska. Fish. Oceanogr. 19:262–278.

Mazur, M. M., M. T. Wilson, A. B. Dougherty, A. Buchheister, and D. A. Beauchamp.
2007. Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. J. Fish Biol. 70:816–836.

Merati, N., and R. D. Brodeur.
1996. Feeding habits and daily ration of juvenile walleye pollock in the western Gulf of Alaska. *In* Ecology of juvenile walleye pollock (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 65–79. NOAA Tech. Rep. NMFS-126.

Pinchuk, A. I., K. O. Coyle, and R. R. Hopcroft.
2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. Prog. Oceanogr. 77:203–216.

Pinchuk, A. I., and R. R. Hopcroft.
2007. Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis, T. spinifera,* and *Euphausia pacifica*) from the northern Gulf of Alaska. Mar. Biol. 151:257–269.

Reed, R. K., and J. D. Schumacher.
1986. Physical oceanography. *In* The Gulf of Alaska physical environment and biological resources (D. W. Hood and S. T. Zimmerman, eds.), p. 57–75. OCS Study MMS86-0095. Minerals Management Service, Springfield, VA.

Schumacher, J. D., and R. K. Reed.
1986. On the Alaska Coastal Current in the western Gulf of Alaska. J. Geophys. Res. 91(C8):9655–9661.

Siegel, V.
2000. Krill (Euphausiacea) life history and aspects of population dynamics. Can. J. Fish. Aquat. Sci. 57(suppl. 3):130–150.

Sogard S.
1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bull. Mar. Sci. 60:1129–1157.

Springer, A. M.
1992. A review: Walleye pollock in the North Pacific—how much difference do they really make? Fish. Oceanogr. 1:80–96.

Wilson, M. T.
2000. Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988. Fish. Bull. 98:823–834.

Wilson, M. T.
2009. Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. Mar. Ecol. Prog. Ser. 392:223–237.

Wilson, M. T., R. D. Brodeur, and S. Hinckley.
1996. Distribution of age-0 walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *In* Ecology of juvenile walleye pollock (R. D. Brodeur, P. A. Livingston, T. R. Loughlin, and A. B. Hollowed, eds.), p. 11–24. NOAA Tech. Rep. NMFS-126.

Wilson, M.T., A. L. Brown, and K. L. Mier.
2005. Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesoscale variation in nursery quality? Fish. Bull. 103:207–218.

Wilson, M. T., C. M. Jump, and A. Buchheister.
2009. Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to krill standing stock and the physical environment. Mar. Ecol. Prog. Ser. 392:239–251.

Wilson, M. T., C. M. Jump, and J. T. Duffy-Anderson.
2006. Comparative analysis of the feeding ecology of two pelagic forage fishes: capelin *Mallotus villosus* and walleye pollock *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 317:245–258.

Wilson, M. T., K. Mier, and A. Dougherty.
2011. The first annulus of otoliths: a tool for studying intra-annual growth of walleye pollock (*Theragra chalcogramma*). Environ. Biol. Fishes. doi:org/10.1007/s/0641-011-9815-1.

Wootton, R. J.
1998. Ecology of teleost fishes, 2nd edn. Fish and fisheries series, vol. 24, 386 p. Kluwer Academic Publs., Dordrecht, The Netherlands.

Yamamura, O., S. Honda, O. Shida, and T. Hamatsu.
2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: ontogenetic and seasonal variations. Mar. Ecol. Prog. Ser. 238:187–198.

Diel and seasonal timing of sound production by black drum (*Pogonias cromis*)

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Abstract—Acoustic recorders were used to document black drum (*Pogonias cromis*) sound production during their spawning season in southwest Florida. Diel patterns of sound production were similar to those of other sciaenid fishes and demonstrated increased sound levels from the late afternoon to early evening—a period that lasted up to 12 hours during peak season. Peak sound production occurred from January through March when water temperatures were between 18° and 22°C. Seasonal trends in sound production matched patterns of black drum reproductive readiness and spawning reported previously for populations in the Gulf of Mexico. Total acoustic energy of nightly chorus events was estimated by integration of the sound pressure amplitude with duration above a threshold based on daytime background levels. Maximum chorus sound level was highly correlated with total acoustic energy and was used to quantitatively represent nightly black drum sound production. This study gives evidence that long-term passive acoustic recordings can provide information on the timing and location of black drum reproductive behavior that is similar to that provided by traditional, more costly methods. The methods and results have broad application for the study of many other fish species, including commercially and recreationally valuable reef fishes that produce sound in association with reproductive behavior.

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Knowledge of the timing and location of spawning provides fundamentally important information for the management of fish species. Traditional methods for acquiring this knowledge have entailed 1) the collection of fishes for examination of spawning condition by means of gonad histology and gonadosomatic indices and 2) the calculation of the time of spawning by back-calculation from the ages of eggs or larvae at the time of collection (Peters and McMichael, 1990; Nieland and Wilson, 1993; Fitzhugh et al., 1993). In some cases direct observations of spawning have been made at fish aggregation sites with the use of scuba, remote cameras, and submersible vehicles (Domeier and Colin, 1997; Erisman and Konotchick, 2009). Although effective, these methods are labor intensive, costly, and not necessarily practical for providing high-resolution data over an entire spawning season or synoptically at multiple sites within a season.

Many fishes produce sounds associated with reproductive behavior, and hydrophone recordings used to document this behavior have been conducted for many years (Breder, 1968; Gilmore, 2003; Mann et al., 2008). Relatively recent advances in technology have made low-cost submersible acoustic recording systems available for recording high-resolution acoustic data over long time periods. These recording systems, along with signal processing algorithms, now represent the most practical method available to collect long-term, high-resolution data on spawning behavior of soniferous fishes, many of which include commercially and recreationally managed species (i.e., drums and groupers [families Sciaenidae and Serranidae, respectively]). Such data can be collected synoptically over wide spatial scales and in remote environments that may not be accessible with other gear types. When acoustic data are combined with environmental data collected on similar time scales, a great deal can be learned about the ecology of sound production and the environmental requirements associated with spawning site selection and spawning behaviors of fishes.

The black drum is a large, long-lived sciaenid that ranges from the Bay of Fundy to Argentina (Hoese and Moore, 1998; Sutter et al.[1]). In the Gulf of Mexico black drum spawn in bays and estuarine habitats from late fall through early spring (Murphy and Taylor, 1989; Peters and McMichael, 1990) and produce high intensity sounds associated with courtship and spawning (Mok and Gilmore, 1983; Saucier and Baltz, 1993; Tellechea et al., 2010) that may exceed 170 dB re: 1µPa (Locascio, 2010). In this study our main objectives were to record and describe patterns of black drum sound production during the spawning season and to compare these data to previous data collected with traditional methods to document the spawning season of black drum.

[1] Sutter, F. C., R. S. Waller, and T. D. McIlwain. 1986. Species profiles: life histories and environmental requirements of coastal fisheries and invertebrates (Gulf of Mexico)—black drum. U.S. Fish. Wildl. Serv. Bio. Rep. 82(11.51, U.S. Army Corps of Eng. TR EL82-4), 10 p.

Materials and methods

Long-term acoustic recording systems (LARS) were deployed in estuarine canals at one site in Punta Gorda and at three sites in Cape Coral, Florida, to document patterns of sound production by black drum (*Pogonias cromis*) during their spawning season. The canals are extensive sea-walled residential systems which allow access to the Gulf of Mexico via Charlotte Harbor (Fig. 1). One LARS was deployed at the Punta Gorda site from 22 March to 3 May 2004, and from 12 December 2004 to 4 May 2005. At Cape Coral sites 1 and 3 (CC1 and CC3), LARS were deployed from 12 February to 6 April 2005, and at Cape Coral site 2 (CC2) from 12 February to 6 May 2005, and from 21 October 2005 to 7 June 2006. These sites were selected on the basis of information provided by canal-side residents of loud booming sounds produced there in the evening during winter months.

Surface and bottom water temperature data were recorded at CC2 during the October 2005–June 2006 deployment with Hobo® temperature data loggers (model UA-002-08; Onset Computer Corp., Bourne, MA) programmed to record data at 10-minute intervals. The surface temperature data logger was attached to a buoy and suspended one half meter below the surface. The bottom temperature data logger was attached to the LARS and recorded data at one half meter above the bottom. All LARS were anchored and remained positively buoyant one half meter above the bottom. Water depth at all sites was approximately seven meters, and the bottom was a soft muddy composite. During the October 2005–June 2006 deployment, the LARS stopped recording after the first week and was reprogrammed and redeployed on 3 December 2005. With this exception all LARS functioned according to schedule during deployments.

Two LARS models were used for recordings: a Persistor CF2 computer (Persistor Instruments Corp., Marston Mills, MA) (sample rate: 2634 Hz) and a Toshiba pocket PC model E755 (Toshiba Computer Corp., Tokyo, Japan) (sample rate: 11,025 Hz). Sample rates used for recording were well above the frequency range where most of the acoustic energy in black drum calls is concentrated (<300 Hz) and therefore aliasing (i.e. under sampling of signals) was not a problem (Locascio, 2010). The Persistor-based LARS was used for all recordings, except for the 21 October 2005–7 June 2006 deployment at CC2. High Tech Inc. (Gulfport, Mississippi) 96-min series hydrophones were used with all LARS (sensitivity: –164dB re: 1V/1µPa and flat frequency response of 2 Hz–37 kHz). The sensitivity of each recorder was calibrated with a 0.1 V peak sinusoidal signal.

Each 10-second file was analyzed with a fast Fourier transform (FFT) to generate a power spectrum from which the band sound pressure level (SPL) in 100-Hz-wide bins was calculated. The SPL was greatest in the 100–200 Hz band and a five-point moving average of data in this frequency range was used for each time series analysis. Black drum calls were identified in recordings by comparison with previously published descriptions by Mok and Gilmore (1983). All data were analyzed with MATLAB, version R2007a software (The Mathworks, Inc., Natick, MA).

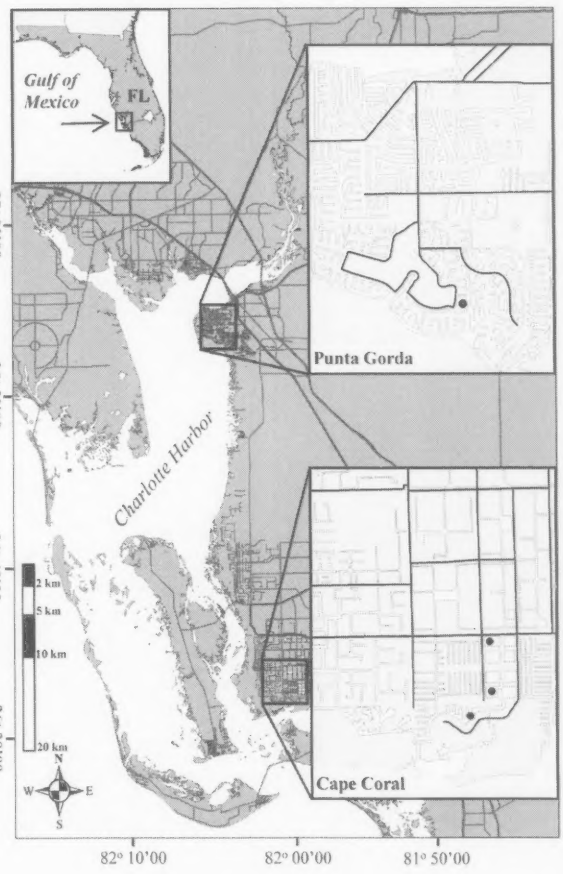

Figure 1

Locations where calls of black drum (*Pogonias cromis*) were recorded in residential estuarine canal systems of Punta Gorda and Cape Coral, Florida. The study sites are indicated by filled black circles. The three study sites in Cape Coral are: CC1 (northernmost); CC2 (central); and CC3 (southernmost).

To be considered a chorus event the SPL was required to exceed an arbitrarily defined threshold of two standard deviations (SD) above the mean daytime background SPL for a minimum of five consecutive recordings (i.e., 50 minutes). Mean daytime SPL was calculated from 0700 to 1500 hours for each site and season separately. Requiring that levels be sustained above the threshold for a minimum of 50 minutes controlled for the infrequent cases where the SPL briefly exceeded the threshold during daytime hours because of vessel noise, weather, or occasional black drum calls.

Table 1

Correlation coefficients (r) and P-values calculated for total acoustic energy (TAE) and maximum sound pressure level (Max SPL), and chorus duration and maximum sound pressure level produced by black drum (*Pogonias cromis*) from each site and season. PG=Punta Gorda, FL; CC=Cape Coral, FL. Mean daily background sound pressure levels and chorus thresholds are expressed as dB SPL (re: 1µPa) of the 100–200 Hz band. df=degrees of freedom, SD=standard deviation.

			Background dB SPL		Chorus threshold	TAE Max SPL		Chorus duration Max SPL	
Site	Dates	df	mean	SD	dB SPL	r	P	r	P
PG	3/22/04–5/3/04	25	85.0	4.1	93.2	0.97	<0.01	0.76	<0.01
PG	12/12/04–5/4/05	82	85.7	4.3	94.3	0.98	<0.01	0.79	<0.01
CC1	2/12/05–4/6/05	42	91.6	3.2	98.0	0.99	<0.01	0.93	<0.01
CC2	2/12/05–5/6/05	102	90.7	3.8	98.3	0.99	<0.01	0.75	<0.01
CC2	12/3/05–6/7/06	42	90.0	3.5	97.0	0.99	<0.01	0.85	<0.01
CC3	2/12/05–4/6/05	39	93.1	3.5	100.1	0.95	<0.01	0.59	<0.01

The threshold was used to mark chorus start and end times from which nightly parameters of chorus duration, total acoustic energy (TAE), and maximum SPL were calculated. TAE (dB re: 1 $\mu Pa^2 \cdot s$) was calculated by converting SPL to µPa and then integrating the acoustic energy (squared acoustic pressure) over the time period that the SPL exceeded the threshold (i.e., by summing the area under the curve). This method is equivalent to the calculation of sound exposure level described by the American National Standards Institute (ANSI, S1.1-1994).

Correlations between TAE and maximum SPL and between chorus duration and maximum SPL were calculated with time series data from each site and for each season. The purpose was to evaluate maximum SPL as a quantitative representation of nightly black drum sound production. Linear regressions were calculated between chorus start time and time of sunset. Correlations between chorus start and end times, between chorus start time and time of maximum SPL, and between chorus start time and maximum SPL were calculated for each time series. Data were tested for normality on the basis of standardized kurtosis and skewness. If data were non-normal, a Spearman nonparametric correlation was calculated instead of a Pearson correlation. The ascending and descending slopes of nightly chorus events were calculated from the chorus start to the time when the sound level first reached 6 dB below maximum SPL and from the time the sound level decreased from 6 dB below maximum SPL to the chorus end. Ascending and descending slopes were compared by using the Wilcoxon signed rank nonparametric test. Correlations between sites for data of chorus start time, chorus end time, chorus duration, and time of maximum SPL were calculated from data recorded concurrently at all sites during 14 February–6 April 2005. Alpha values were adjusted by using sequential Bonferroni tests to correct for experiment-wise error (Sokol and Rolf, 1995). Cross correlations between nightly maximum SPL and surface and bottom water temperature were calculated for the 2005–06 CC2 time series. Fourier analysis was used to examine for patterns of lunar periodicity in black drum sound production in the Punta Gorda time series recorded during December 2004–May 2005 and the CC2 time series recorded during October 2005–June 2006.

Results

Total acoustic energy (TAE) and maximum sound pressure level (SPL), and chorus duration and maximum SPL, were positively and significantly correlated for all sites and seasons (Table 1). The high association between TAE and maximum SPL (r=0.95 to 0.99) qualified maximum SPL to quantitatively represent black drum sound production on a nightly basis. The gulf toadfish (*Opsanus beta*) was the only other soniferous fish recorded. The call of this species has a fundamental frequency of approximately 280Hz (Thorson and Fine, 2002) and therefore did not contribute to the SPL calculated in the 100–200 Hz frequency band used for analysis of black drum acoustic data. Invertebrate sounds (so called "snapping-shrimp") were not recorded at the study sites.

Black drum sound production was strongly periodic. Calls were occasionally recorded during the mid-morning through early afternoon but increased sharply from late afternoon to early evening, and chorus duration lasted up to 12 hours during peak season (Fig. 2). Regressions of chorus start time and time of sunset resulted in higher r^2 values for the shorter time series, which began during the mid to late season in February 2005 (CC1, CC2, CC3) and March 2004 (PG) (r^2=0.39 to 0.54), than for the two longer time series which covered the majority of the season, CC2 2005–06 (r^2=0.04) and PG 2004–05 (r^2=0.02). Data used for all correlations were normally distributed, except for chorus start time data from CC3. Chorus start and end times were negatively and in most cases significantly correlated and indicated that later start times

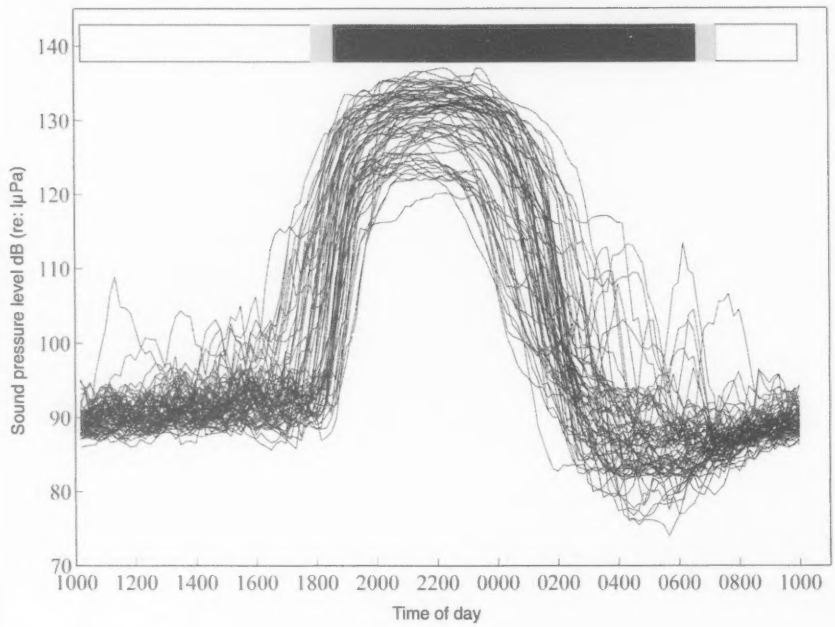

Figure 2

Diel periodicity of black drum (*Pogonias cromis*) sound production (expressed as sound pressure level) represented by an overlay plot of consecutive 24-hour periods recorded from 15 February–16 March 2005 at Cape Coral site 2. The white portion of the diel bar at the top of the figure represents daylight hours, the black represents night hours, and the gray represents time of sunset and sunrise over the dates when these data were recorded.

Table 2

Regression coefficients (r^2) and *P*-values calculated for chorus start time vs. time of sunset, and correlation coefficients (*r*) and *P*-values calculated for chorus start time and chorus end time, chorus start time and time of maximum SPL (Max SPL), and chorus start time and maximum SPL produced by black drum (*Pogonias cromis*). Asterisks denote a Spearman correlation was calculated instead of a Pearson correlation. PG=Punta Gorda, FL; CC=Cape Coral, FL. df=degrees of freedom.

			Chorus start time time of sunset		Chorus start time chorus end time		Chorus start time time of max SPL		Chorus start time max SPL	
Site	Dates	df	r^2	*P*	*r*	*P*	*r*	*P*	*r*	*P*
PG	3/22/04–5/3/04	25	0.41	<0.01	−0.65	0.01	0.28	0.12	−0.67	<0.01
PG	12/12/04–5/4/05	82	0.02	0.33	−0.56	<0.01	0.19	0.10	−0.74	<0.01
CC1	2/12/05–4/6/05	42	0.54	<0.01	−0.34	0.03	0.41	0.06	−0.78	<0.01
CC2	2/12/05–5/6/05	102	0.43	<0.01	−0.28	0.07	0.38	0.01	−0.78	<0.01
CC2	12/3/05–6/7/06	42	0.04	0.06	−0.61	<0.01	0.02	0.81	−0.85	<0.01
CC3	2/12/05–4/6/05	39	0.39	<0.01	*−0.27	0.10	*0.31	0.06	*−0.56	<0.01

generally meant earlier end times, and conversely, that earlier start times were associated with later end times (Fig. 3, Table 2). Correlations of chorus start time and maximum SPL were strongly negative and significant for comparisons of all time series and indicated that earlier chorus start times were associated with higher maximum SPL; however, chorus start time and time of maximum SPL were only weakly and slightly positively correlated (Table 2). Monthly mean chorus start and end times were more variable than the monthly mean

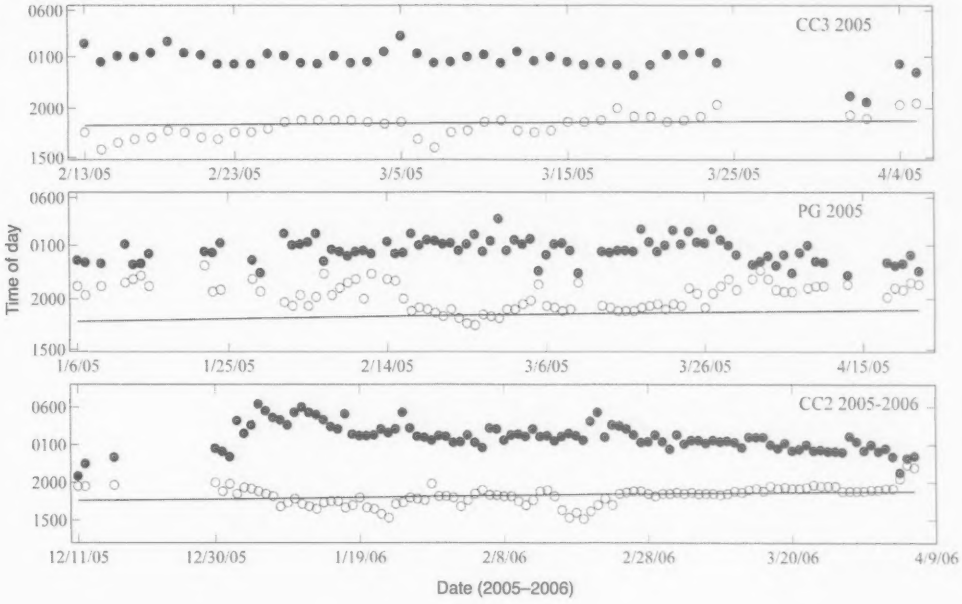

Figure 3

Times of chorus start (open circles), chorus end (filled circles), and sunset (solid line) for select time series of black drum (*Pogonias cromis*) sound production recorded at Cape Coral site 3 (CC3, top graph) and Punta Gorda (PG, middle graph) during 2005, and Cape Coral site 2 (CC2, bottom graph) during 2005–06. (Further details are given in Tables 2 and 3).

Table 3

Wilcoxon signed-rank test statistics (*T*) and *P*-values of ascending vs. descending slopes and mean and standard deviation (SD) of black drum (*Pogonias cromis*) chorus events. Slopes were measured from chorus start time to 6 dB below maximum sound production level (SPL) (ascending) and from 6 dB below maximum SPL to chorus end time (descending). Ascending slopes were significantly greater for each time series. PG=Punta Gorda, F; CC=Cape Coral, FL. df=degrees of freedom.

			Chorus ascending slope		Chorus descending slope			
Site	Dates	df	mean	SD	mean	SD	Wilcoxon *P*	Wilcoxon *T*
PG	3/22/04–5/3/04	25	2.10	0.80	1.50	0.85	0.03	2.4
PG	12/12/04–5/4/05	82	2.40	1.44	1.70	1.10	<0.01	3.1
CC1	2/12/05–4/6/05	42	3.10	1.32	1.70	0.62	<0.01	6.0
CC2	2/12/05–5/6/05	102	2.90	0.95	2.30	0.87	0.01	2.7
CC2	12/3/05–6/7/06	42	3.00	1.42	1.80	0.90	<0.01	7.9
CC3	2/12/05–4/6/05	39	1.80	0.85	1.20	0.88	<0.01	3.2

time of maximum SPL. Ascending chorus slopes were significantly greater than descending slopes for all time series (Table 3).

A distinct seasonal pattern was evident in black drum sound production in all acoustic time series, and sound production patterns were consistent between years for each site (Figs. 4 and 5, Table 4). Subchorus threshold levels of black drum calls were recorded as early as the third week of October (at CC2 in 2005) and as late as the first week of May (at PG in 2004). Sound production first exceeded threshold levels by mid December in CC and early January in PG and were last recorded in early and late April, respectively (Table 4). Monthly mean maximum SPLs were greatest during January

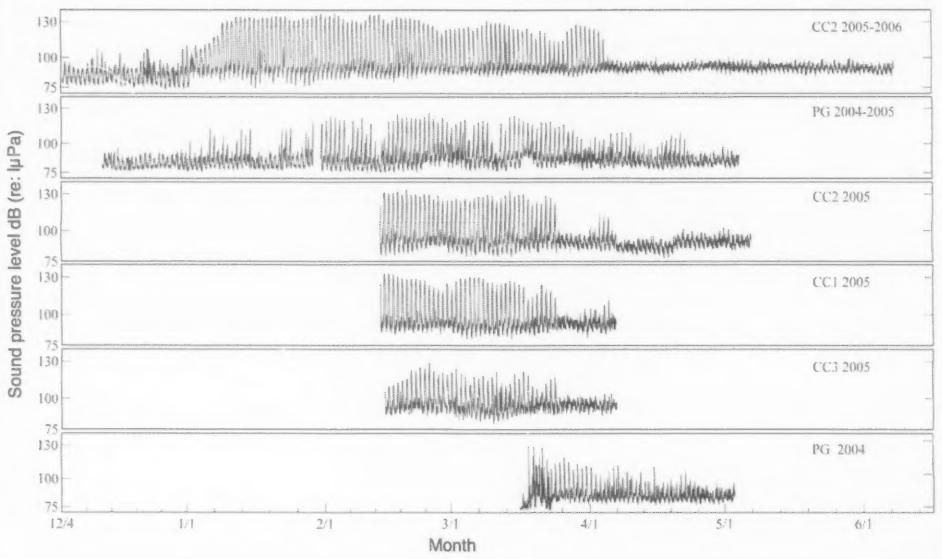

Figure 4

Acoustic time-series data of black drum (*Pogonias cromis*) sound production from all sites and years. Sound pressure level (SPL) was calculated as dB band level of 100 – 200 Hz (re: 1µPa) from 10-second recordings made every 10 minutes. Increased nightly SPLs (evident as peaks in the data) during winter through early spring are consistent with the black drum spawning season and are similar between study areas and years. CC=Cape Coral, FL, and PG=Punta Gorda, FL

and February at the CC sites and during February and March at the PG site (Figs. 4, and 5).

The CC2 2005–06 time series began and ended somewhat abruptly relative to chorus threshold levels. Data recorded at each of the CC sites during 2005 revealed a similar pattern at the end the season. In contrast, maximum SPL recorded during both years at the PG site increased and decreased more gradually at the start and end of each season and sound production continued for two to three weeks longer than at the CC sites. Maximum SPLs at PG were also generally lower and more variable than at the CC sites (Figs. 4 and 5, Table 4).

The greatest coefficient produced by the cross correlation of maximum SPL and bottom temperature was –0.81 at 0 days lag. The correlation coefficient produced by surface temperature and maximum SPL at 0 days lag was –0.14 and the greatest coefficient was –0.4 at 22 days lag. Surface temperatures ranged from approximately 17.5° to 26°C during the seasonal period of black drum sound production (4 December 2005–10 April 2006) but fluctuated within a range of about 18° to 22°C during 4 December 2005–20 February 2006 ($\bar{x}$=20.3, standard deviation [SD]=1.8, n=78) and 22.5° to 26°C ($\bar{x}$=23.9, SD=1.2, n=48) during 21 February–10 April 2006. Surface temperatures during these two periods were significantly different (t=–14.8, P<0.01). Cross correlations between maximum SPL and surface temperature produced maximum correlation coefficients of –0.33 at two days lag for 4 December 2005–20 February 2006 and –0.69 at one day lag for 21 February–10 April 2006. Bottom temperatures ranged from approximately 17° to 24°C over the entire time series and were less variable than surface temperatures. The seasonal peak in maximum SPL occurred when surface and bottom temperatures were both between 18° and 22°C during early January through late February. Time series data of maximum SPL and corresponding temperature data for CC2 are shown in Figure 6.

Chorus start, end, and duration were positively correlated between all sites, except PG and CC1 (Table 5). A stronger association existed among the Cape Coral sites for each of these variables and in particular for chorus start time (Fig. 7). The time of maximum SPL was weakly correlated between sites (either slightly positive or negative and insignificant). The FFT results of maximum SPL data did not indicate that black drum sound production occurred on a lunar cycle.

Discussion

The black drum spawning season has been defined within the Gulf of Mexico through histological examination of oocyte development, gonadosomatic indices, and collection of eggs, larvae, and juveniles (Murphy

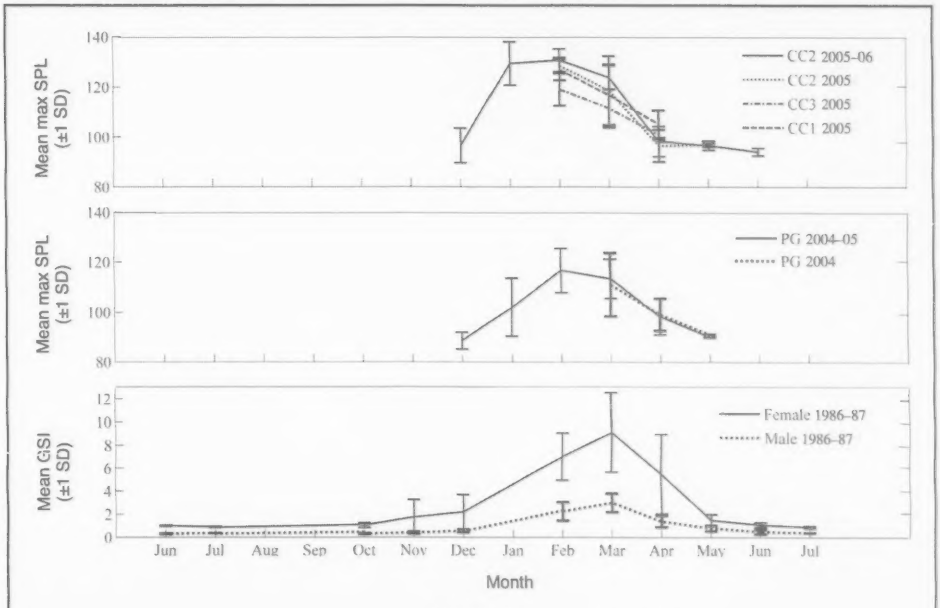

Figure 5

Monthly means and standard deviations (SD) of sound pressure level (SPL) data for black drum (*Pogonias cromis*) from all sites and years (top two graphs) along with gonadosomatic index (GSI) data reprinted from Fitzhugh et al., 1993 (bottom graph). Patterns of black drum sound production are in general agreement with patterns in the GSI data collected from coastal waters of Louisiana. The peak in GSI data occurs slightly later in the season than peaks in sound production recorded in southwest Florida because of the influence of latitude and water temperature on spawning and sound production. CC=Cape Coral, FL, and PG=Punta Gorda, FL

and Taylor, 1989; Peters and McMichael, 1990; Nieland and Wilson, 1993; and Fitzhugh et al., 1993). Results of these studies are in general agreement and have shown that the spawning season occurs from late fall through early spring and that peak spawning occurs during February and March, given some variability with latitude. Seasonal patterns of black drum sound production recorded in this study are consistent with the timing of the spawning season defined in the literature and show that passive acoustics can be as effective as traditional methods for documenting the seasonal reproductive period of black drum. Figure 5 features data of gonadosomatic indices of black drum, reprinted from a study by Fitzhugh et al., (1993) which illustrate the relationship between reproductive condition and sound production during the spawning season.

Although the time series of black drum sound production at all sites and for all years conformed to the same general seasonal pattern, clear similarities and differences existed among them. Sound production at PG varied between the 2004 and 2005 seasons by only one day for the date of the last chorus and four days for the date of the last recorded black drum call. The dates of the last recorded chorus and call were identical among CC sites during 2005 and differed from the CC2 2006 time series by only two and five days, respectively. Sound production consistently lasted two to three weeks longer at the PG site than at the CC sites. We do not have data to explain the similarities between years at the same sites or the differences that existed between the PG and CC sites, but the simplest explanation could be that water temperatures were responsible for these patterns. The PG and CC sites are only 40 km apart and therefore the influence of latitude alone may not be responsible for differences in water temperature. It is possible that local effects such as exposure to sun, wind, and influence of adjacent water bodies may have contributed to the temperature differences responsible for the later end to seasonal calling in PG.

Differences were also evident in the lower and more variable maximum SPLs recorded at PG and CC3 and these may be associated with the distribution of calling fish relative to hydrophone locations. Because black drum source levels do not appear to be highly variable among individuals (Locascio, 2010) the patterns of maximum SPL at these sites may not be due to lower intensity calls, but rather to calls from fish at greater or more variable distances from the hydrophone. Both sites were located within smaller, narrower areas of the canal systems compared to the locations of CC1 and

CC2 and may have accommodated fewer fish especially if (male) black drum establish territories which require some space between individuals (Locascio, 2010). Another interesting pattern was apparent in the correlation of synoptically recorded data from all sites. The higher correlations among the CC sites for chorus timing revealed that acoustic signaling by black drum may occur in the context of a communication network, where the calling behavior initiated by some individuals elicits responses from others and propagates throughout the population. We were not able to confirm this pattern in the Punta Gorda canal system because of having only one study site there. It is also possible that some overarching environmental condition(s) helped initiate calling at each of the three Cape Coral sites. These results emphasize the need that complementary environmental data be collected along with acoustic data.

In two previous studies, hydrophone recordings were used to investigate black drum spawning behavior. Saucier and Baltz (1993) conducted mobile hydrophone surveys in coastal southeast Louisiana and recorded black drum calls from January through April, in 15.0° to 24.0°C water temperatures, and peak sound production in March and April. The highest SPLs were recorded in 20.8°C (±1.01) and 18.9°C (±1.43) water temperatures for presumed large and moderate-size black drum aggregations, respectively. Mok and Gilmore (1983) also conducted mobile hydrophone surveys and recorded black drum during the winter and early spring in Indian River Lagoon, Florida. They reported maximal sound production during January in 18.0° to 20.0°C water temperatures and no sound production occurred below 15.0°C. Although water temperature did not reach the apparent 15.0°C lower limit for sound production in our study, the temperature range over which black drum were recorded (bottom: 17–24°C, surface: 17.5–26°C) and the range associated with highest levels of sound production (18–22°C) are consistent with these previous studies. Black drum are a demersal species which would account for the higher correlation between SPL and bottom water temperatures in this study. The higher correlation between surface water temperatures at a one day lag and sound production during the latter half of the season could indicate that black drum were higher in the water column or possibly that this was a response to increasing photoperiod, which would be positively correlated with temperature.

The range of water temperatures associated with black drum sound production has also been reported for spawning. Peters and McMichael (1990) back-calculated larval black drum birthdates from collections made in Tampa Bay, FL, and estimated that water temperatures were 16–20°C during the early part of the spawning season and 21–24°C during peak season. Holt et al. (1988) collected black drum eggs in water temperatures of 18–25°C in the Gulf of Mexico near Port Aransas, Texas. Within the geographic range of black drum in U.S. waters, spawning has been documented to occur later in the year at more northern latitudes (Murphy and Taylor, 1989) but apparently within the

Table 4

Monthly means and standard deviations (SD) of the maximum sound pressure level (dB re:1μPa) of the 100–200 Hz band recorded at each site and season and dates of the last black drum (*Pogonias cromis*) chorus and last recorded black drum calls. The last acoustic activity of black drum occurred on similar dates of different years at each study site. PG=Punta Gorda, FL; CC=Cape Coral, FL.

		December		January		February		March		April		May			
Site	Dates	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	Last chorus	Last call
PG	3/22/04–5/3/04							111.0	12.6	99.1	6.5	91.0	0.0	4/21/2004	5/1/2004
PG	12/12/04–5/4/05	88.4	3.4	101.9	11.6	116.7	8.9	113.4	7.8	98.3	7.4	90.1	0.4	4/22/2005	4/27/2005
CC1	2/12/05–4/6/05					126.9	4.2	116.8	12.3	105.2	5.5			4/4/2005	4/5/2005
CC2	2/12/05–5/6/05					128.5	3.1	118.6	13.7	96.6	6.4	96.9	0.7	4/4/2005	4/5/2005
CC2	12/3/05–6/7/06	96.6	7.0	129.4	8.6	130.7	4.5	123.8	4.8	98.3	6.0	96.6	1.7	4/6/2006	4/10/2006
CC3	2/12/05–4/6/05					119.0	6.5	111.5	7.7	101.0	2.0			4/4/2005	4/5/2005

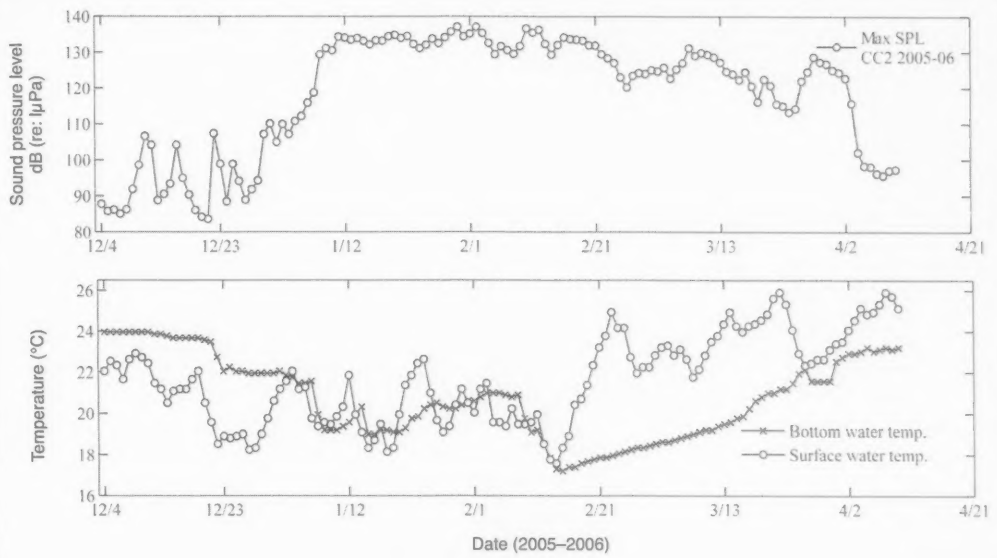

Figure 6

Nightly maximum sound pressure level (SPL) data for black drum (*Pogonias cromis*) calls from the Cape Coral site 2 (CC2) 2005–06 time series (top graph) and bottom and surface water temperature data (bottom graph) recorded every ten minutes during the period 4 December 2005–10 April 2006.

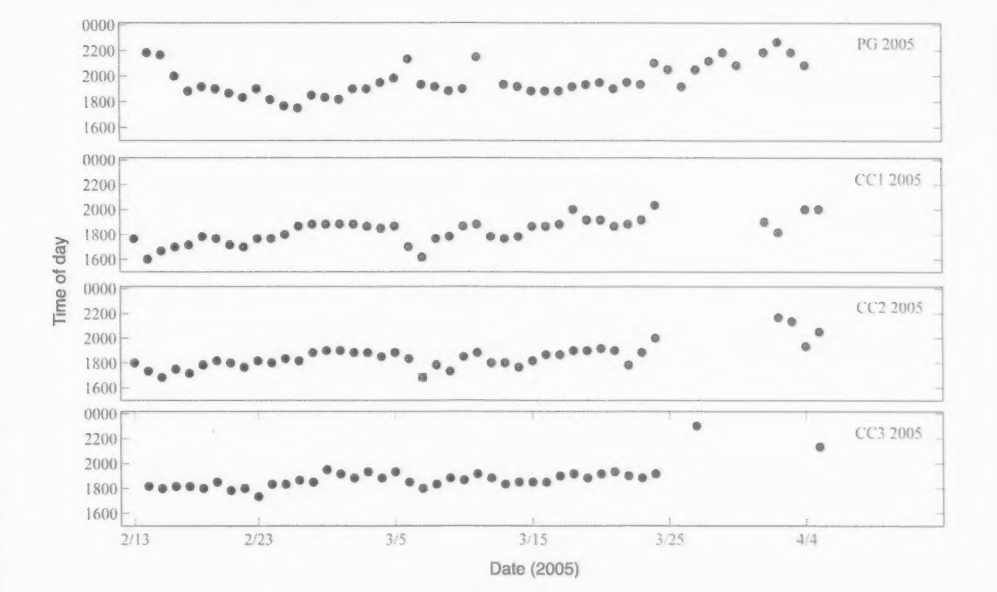

Figure 7

Synoptically recorded data of chorus start time of black drum (*Pogonias cromis*) sound production from all study sites. Data recorded at the Cape Coral (CC) sites were highly correlated with each other but not with data recorded at the Punta Gorda site (PG) (details are given in Table 5).

Table 5

Correlation coefficients (r) and P-values calculated for chorus parameters determined for black drum (*Pogonias cromis*) from synoptically recorded acoustic data at all study sites. Asterisks denote alpha values adjusted for experiment-wise error. PG=Punta Gorda, FL; CC=Cape Coral, FL. df=degrees of freedom.

	Chorus start time			Chorus end time			Chorus duration			Time of max SPL		
Sites	df	r	P	df	r	P	df	r	P	df	r	P
PG, CC1	40	−0.06	0.71	39	0.31	0.05	40	0.15	0.35	39	0.21	0.21
PG, CC2	40	0.37	*0.02	40	0.29	0.07	40	0.41	0.01	40	−0.08	0.64
PG, CC3	38	0.16	0.34	38	0.32	*0.05	38	0.26	0.11	38	0.12	0.48
CC1, CC2	42	0.72	<0.01	42	0.57	<0.01	42	0.79	<0.01	42	0.19	0.24
CC1, CC3	39	0.72	<0.01	39	0.38	0.02	39	0.52	<0.01	39	−0.02	0.91
CC2, CC3	39	0.77	<0.01	39	0.61	<0.01	39	0.69	<0.01	39	−0.10	0.53

same water temperature range regardless of latitude. In Chesapeake Bay for example, black drum spawn from late April through June (Wells and Jones, 2002) when water temperatures are within approximately the same range as that reported for the Gulf of Mexico during the spawning season (MDNR[2]). Johnson (1978) estimated that black drum spawning at the mouth of Chesapeake Bay probably occurred in water temperatures of 15–21°C. Spawning by black drum later in the year at higher latitudes (June in Chesapeake Bay), but in the same water temperature range that occurs in Florida during February, indicates that temperature may be more influential than photoperiod on black drum reproduction.

Peters and McMichael (1990) noted that peak spawning occurred around new and full moons and suggested this was due to increased tidal amplitude. We found no patterns in lunar periodicity associated with black drum sound production, but because the precise relationship between the timing of sound production and spawning has not yet been explained for black drum, it is possible that these different behaviors may vary on lunar (or other) time scales. Associations with moon phase and fish sound production have been reported (Breder, 1968; Gilmore, 2003; Mann et al,. 2008). Aalbers (2008) found increased that calling rates were associated with spawning by white seabass, which occurred throughout the lunar cycle but more so at the time of the new moon to four days after.

Establishing chorus start and end times at two standard deviations above mean daytime levels is a conservative approach for measuring chorus timing parameters because the earliest and latest parts of the chorus are ignored. Still, there was sufficient variability in chorus duration over the course of the season to show the strong association between TAE and maximum SPL. Although TAE would appear to be a better choice to quantitatively represent nightly black drum sound production because it is a more comprehensive measure, maximum SPL has the advantage of not depending on the threshold level that is chosen, whereas TAE tends to increase at lower threshold levels. The correlation between maximum SPL and chorus duration was not as strong as that between maximum SPL and TAE because threshold points from which chorus duration was measured did not account for variability in duration of signal amplitude above threshold as did the TAE calculation. In a previous study, we found a weak negative relationship between maximum SPL and chorus duration of sand seatrout (*Cynoscion arenarius*) (r=−0.24) (Locascio and Mann, 2008). The relatively low correlation among *C. arenarius* data was because they were collected during peak spawning season when signal amplitude and chorus duration were consistently high and variability was low compared to the range that exists when data are recorded across an entire spawning season as in this study (with *P. cromis*).

Black drum exhibited a diel pattern of sound production consistent with general descriptions found in the literature for many fishes that produce sound associated with courtship and spawning. Calling levels increase rapidly within an hour or two before sunset and reach maximal levels within a few hours after dusk (Breder, 1968; Mok and Gilmore, 1983; Luczkovich et al., 1999; Aalbers, 2008). In the previous hydrophone studies by Saucier and Baltz (1993) and Mok and Gilmore (1983), black drum calling was noted as early as 1300 and 1400 h, respectively, and the majority of sound production occurred between 1800 and 2200 h. The earliest chorus start time in this study occurred at 1510 h on 19 February 2005 at CC2, but individual calls were occasionally recorded throughout the day during peak season.

Earlier chorus start times occurred during the peak spawning season and generally corresponded to later end times and higher maximum SPLs (Table 2). This pattern, along with later chorus start times at the beginning and end of the season, was responsible for the low r^2 from the regression with time of sunset for the two longer time series. Connaughton and Taylor (1995) discovered a similar pattern of high intensity calling earlier in the day that lasted later into the evening

[2] MDNR (Maryland Department of Natural Resources), www.eyesonthebay.net, accessed Dec. 2009.

during the peak spawning season of weakfish. They noted physiological indicators of reproductive readiness in weakfish, including increased plasma androgen levels and hypertrophy of sonic muscle in males, were evident during the seasonal period of maximal sound production and spawning. This pattern has also been documented for spotted seatrout (Brown-Peterson, 2003) and toadfish (Fine and Pennymaker, 1986). It is likely that similar conditions exist in black drum and contribute to earlier and increased sound production during the peak seasonal reproductive period.

For each time series the ascending slope was significantly greater than the descending slope of choruses. The more gradual changes associated with the descending slope of the chorus event may be due to fewer individuals calling. This may be a consequence of sonic muscle fatigue, but it may also be related to fluctuations in hormone levels, as demonstrated on a seasonal time frame for weakfish. Monthly mean values of time of maximum SPL were not highly variable despite the relatively high variability in chorus start and end times. Rates of SPL change during chorus events are not available in the literature, although in cases where sufficient diel time series data have been collected authors have observed a relatively rapid onset of calling and substantial increase in SPL over moderately short time periods (Breder, 1968; Connaughton and Taylor 1995; Locascio and Mann, 2008; Mann et al., 2008). One mechanism for this increase in SPL may be that an individual's calls elicit responses from other individuals and result in rapidly increased SPL as calling activity spreads throughout the network of fish. This mechanism has been proposed to serve as a means of aggregating individuals for spawning while creating the opportunity among (male) individuals to compete acoustically for a chance at reproduction. Some evidence indicates that calling rates of individuals are not highly variable (Connaughton and Taylor, 1995; Locascio, 2010) and therefore increased SPL and calling rates of a group may be due to more individuals calling, as opposed to individuals calling more (Connaughton and Taylor, 1995). More data are needed to understand how frequencies and sound levels and calling rates vary among individuals of a species. Variation in fundamental frequencies of black drum calls with body size has been shown by Tellechea et al. (2010).

Conclusions

This study revealed that the timing and amplitude of black drum sound production is strongly correlated with the seasonal spawning period described in the literature. Long-term acoustic recording systems can therefore be used to complement traditional methods for defining the spawning season, are much less expensive, and produce high-resolution time series data. These recording systems are an especially useful and cost-effective tool for exploring new and remote locations where the formation of spawning aggregations is suspected or for monitoring the recovery of historical spawning sites. Inferences about habitat quality can also be made from acoustic data because spawning site selection should place early life history stages in habitats beneficial for growth and survival (Peebles and Tolley, 1988). In order to advance the use of passive acoustic methods future studies must focus on establishing quantitative relationships between sound production and spawning, the number and biomass of spawning individuals, and environmental parameters. Also required is a more detailed understanding of the behavior associated with sound production and the identification of currently unidentified sound- producing species.

Literature cited

Aalbers, S. A.
2008. Seasonal, diel, and lunar spawning periodicities and associated sound production of white seabass (*Atractoscion nobilis*). Fish. Bull. 106:143–151.

American National Standards Institute.
1994. Acoustical terminology, 9 p. Standards Secretariat, Acoustical Soc. America, New York. ANSI-S1.1-1994.

Breder, C. M.
1968. Seasonal and diurnal occurrences of fish sounds in a small Florida bay. Bull. Am. Mus. Nat. Hist. 138:327–378.

Brown-Peterson, N.
2003. The reproductive biology of spotted seatrout. *In* The biology of seatrout (S. A. Bortone, ed.), p. 99–133. CRC Press, Boca Raton, FL.

Connaughton, M. A., and M. H. Taylor.
1995. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. Environ. Biol. Fishes 42:233–240.

Domeier, M. L., and P. L. Colin.
1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60 698–726.

Erisman, B. E., and T. H. Konotchick.
2009. Observations of spawning in the leather bass, *Dermatolepis dermatolepis* (Teleostei: Epinephelidae), at Cocos Island, Costa Rica. Environ. Biol. Fishes 85:15–20.

Fine, M. L., and K. R. Pennymaker.
1986. Hormonal basis for sexual dimorphism of the sound-producing apparatus of the oyster toadfish. Exp. Neurol. 92:289–298.

Fitzhugh, G. R., B. A. Thompson, and T. G. Snider III.
1993. Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana. Fish. Bull. 91:244–253.

Gilmore, R. G., Jr.
2003. Sound production and communication in the spotted seatrout. *In* Biology of the spotted Seatrout (S. A. Bortone, ed.), p. 177–195. CRC Press, Boca Raton, FL.

Hoese, H. D., and R. H. Moore.
1998. Fishes of the Gulf of Mexico, Texas, Louisiana and adjacent waters, 422 p. Texas A&M Univ. Press, College Station, TX.

Holt, S. A., G. J. Holt, and L.Young-Abel.
1988. A procedure for identifying sciaenid eggs. Contrib. Mar. Sci. (suppl.) 30:99–108.

Johnson, G. D.
1978. *Pogonias cromis*, black drum. *In* Development of fishes of the mid-Atlantic bight: an atlas of egg, larval, and juvenile stages, vol. IV: Carangidae through Ephippidae (G. D. Johnson, ed.), p. 235–237. U.S. Fish and Wildlife Service, Dept. of the Interior, Washington D.C.

Locascio, J. V., and D. A. Mann.
2008. Diel periodicity of fish sound production in Charlotte Harbor, Florida. Trans. Am. Fish. Soc. 137:606–615.
2010. Passive acoustic studies of estuarine fish populations of southwest Florida. Ph.D. diss., 201 p. College of Marine Science, Univ. South Florida, St. Petersburg, FL.

Luczkovich, J. J., M. W. Sprague, S. E. Johnson, and R. C. Pullinger.
1999. Delimiting spawning areas of weakfish *Cynoscion regalis* (family Sciaenidae) in Pamlico Sound, North Carolina, using passive hydroacoustic surveys. Bioacoustics 10:143–160.

Mann, D. A., J. V. Locascio, F. C. Coleman, and C. K. Koenig.
2008. Goliath grouper *Epinephelus itajara* sound production and movement patterns on aggregation sites. Endang. Species. Res. 7:229–236.

Mok, H. K., and R. G. Gilmore.
1983. Analysis of sound production in estuarine aggregations of *Pogonias cromis*, *Bairdiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). Bull. Inst. Zool. Academica Sinica 22:157–186.

Murphy, M. D., and R. G. Taylor.
1989. Reproduction and growth of black drum, *Pogonias cromis*, in northeast Florida. Northeast. Gulf. Sci. 10:127–137.

Nieland, D. L., and C. A. Wilson.
1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 122(3):318–327.

Peebles, E. B., and S. G. Tolley.
1988. Distribution, growth and mortality of larval spotted seatrout, *Cynoscion nebulosus*: A comparison between two adjacent estuarine areas of southwest Florida. Bull. Mar. Sci. 42:397–410.

Peters, K. M., and R. H. McMichael.
1990. Early life history of the black drum *Pogonias cromis* (Pisces: Sciaenidae) in Tampa Bay, Florida. Northeast. Gulf. Sci. 11:39–58.

Saucier, M. H., and D. M. Baltz.
1993. Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. Environ. Biol. Fishes 36:257–272.

Sokol, R. R., and J. F. Rolf.
1995. Biometry, 3rd ed., 887 p. W.H. Freeman, New York.

Tellechea, J. S., W. Norbis, D. Olsson, and M. L. Fine.
2010. Calls of the black drum (*Pogonias cromis*: Sciaenidae): geographical differences in sound production between northern and southern hemisphere populations. J. Exp. Zool. 313A:48–55.

Thorson, R. F., and M. L. Fine.
2002. Crepuscular changes in emission rate and parameters of the boatwhistle advertisement call of the gulf toadfish, *Opsanus beta*. Environ. Biol. Fishes 63:321–331.

Wells, B. K., and C. M. Jones.
2002. Yield-per-recruit analysis for black drum, *Pogonias cromis*, along the east coast of the United States and management strategies for Chesapeake Bay. Fish. Bull. 99:328–337.

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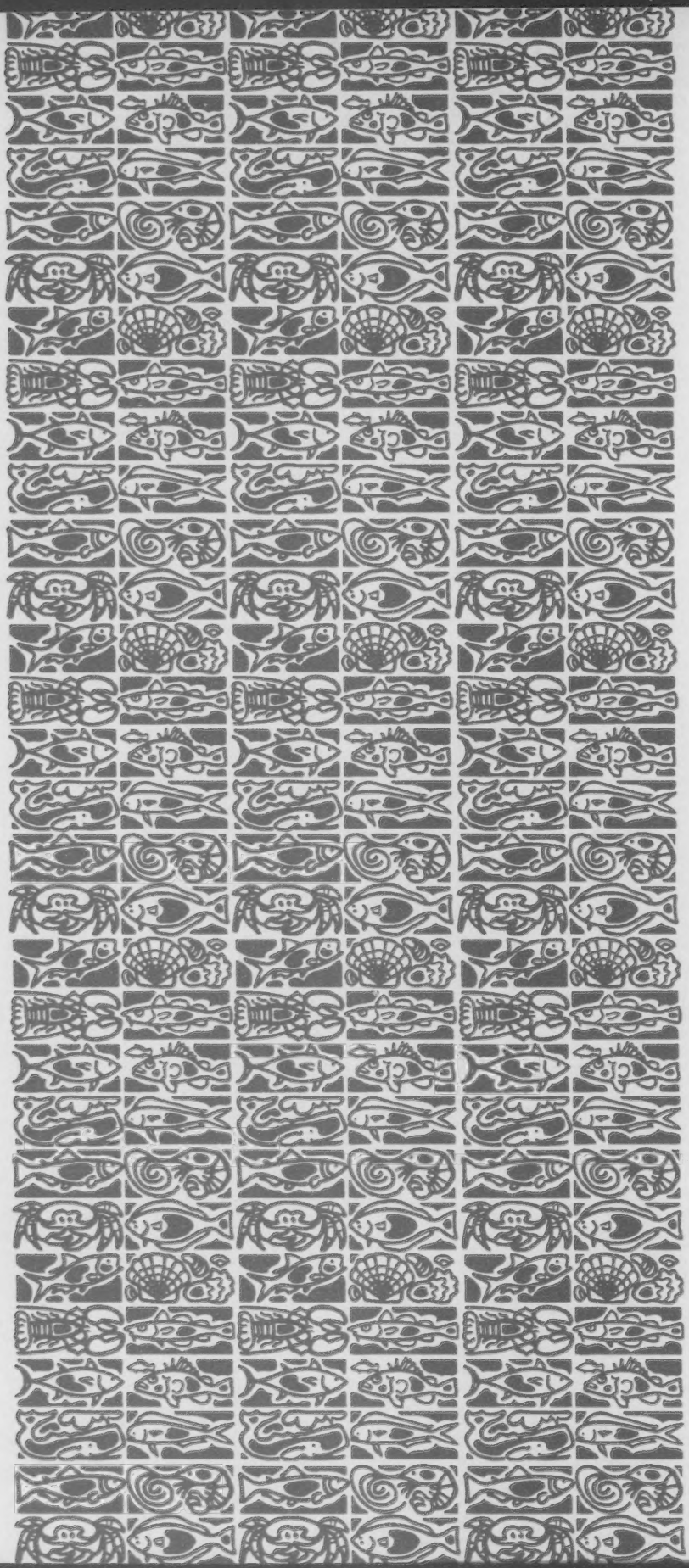
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